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SIGNIFICANCE OF NEARSHORE TRACE-FOSSIL ASSEMBLAGES OF THE
CAMBRO-ORDOVICIAN DEADWOOD FORMATION AND
ALADDIN SANDSTONE, SOUTH DAKOTATHOMAS M. STANLEY¹RODNEY M. FELDMANN²

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ABSTRACT

The Cambro-Ordovician Deadwood Formation and Aladdin Sandstone represent intertidal and subtidal, nearshore deposystems that contain few well-preserved body fossils, but contain abundant trace fossils. The present study uses the much neglected trace-fossil fauna to describe the diverse paleoenvironments represented in the Deadwood-Aladdin deposystems, and to better understand the environmental conditions that controlled benthic life in the Early Paleozoic.

The Deadwood-Aladdin ichnotaxa can be separated into three distinct assemblages based on the changing sedimentologic and hydrodynamic conditions that existed across the Cambro-Ordovician shelf. Trace-fossil assemblages and corresponding lithofacies characteristics indicate that the Deadwood-Aladdin deposystems formed within an intertidal-flat and subtidal-shelf environment.

Based on the distribution and numbers of preserved ichnotaxa, the intertidal flat can be subdivided further into an ecologically stressful inner sand-flat environment, and a more normal marine outer sand-flat environment, both of which belong to a mixed, *Skolithos*-*Cruziana* softground ichnofacies. The inner sand flat is characterized by low diversity, low numbers, and a general lack of complexly constructed ichnotaxa. Trace fossils common to both assemblages tend to be smaller in the inner flat compared to the outer sand flat. Taphonomic effects, such as substrate type and sediment heterogeneity, also aid in differentiating between the inner and outer sand-flat assemblages.

The subtidal shelf environment is categorized in the *Cruziana* ichnofacies. Ichnological evidence of periodic tempestite deposition and hardground development within this subtidal regime is manifested by high diversity and low abundance of ichnogenera.

KEY WORDS: trace fossils, ichnofossils, Cambrian, Ordovician, South Dakota, ichnofacies

INTRODUCTION AND HISTORICAL PERSPECTIVE

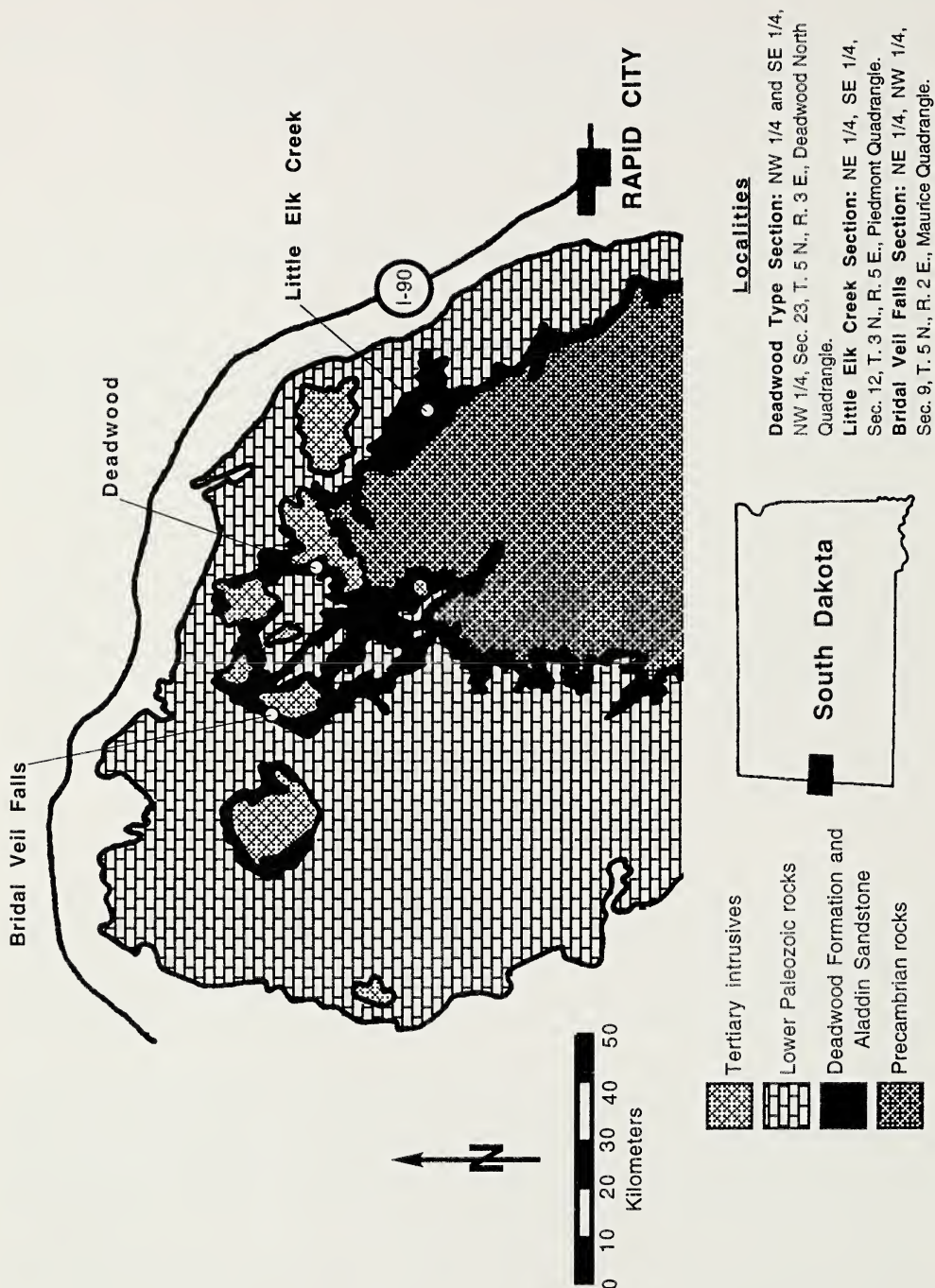
The Deadwood Formation and Aladdin Sandstone comprise all the Upper Cambrian and most of the lowermost Ordovician rocks in western North Dakota and South Dakota, and eastern Montana and Wyoming. Surface exposures are limited to the Black Hills region of western South Dakota and eastern Wyoming, where they form an elliptical outcrop pattern within the interior of the Black Hills uplift (Fig. 1).

The Deadwood Formation was formally named by Darton (1909) for exposures at Deadwood, South Dakota. The stratotype included the Deadwood Formation, Aladdin Sandstone, and basal lithotypes of what is now known as the lowermost Ordovician Winnipeg Formation (Fig. 1, 3). Because of the paucity of body fossils, Darton (1909) could only ascribe a Cambrian age to the type section. With continued paleontologic study of enclosed trilobites, the "Deadwood Formation"

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was given a Late Cambrian age by Darton and Paige (1925). Later, Furnish et al. (1936) separated the overlying Winnipeg Formation from the Deadwood Formation based on the presence of Early Ordovician conodonts. Subsequently, Lochman and Duncan (1950) found Early Ordovician trilobites in the upper intraclastic limestones in several "Deadwood" sections. Because no obvious unconformity exists between Cambrian and Ordovician strata, the Deadwood Formation was reassigned a Late Cambrian–Early Ordovician age. The current stratigraphic picture was completed by McCoy (1952) who designated the upper 4.4 m of the Deadwood Formation as the Aladdin Sandstone based on the presence of numerous *Skolithos* burrows.

Since its first description, investigators of the Deadwood Formation have commented on the abundant trace fossils that occur within the unit (Darton, 1909; Darton and Paige, 1925). Although trace fossils represent the dominant faunal evidence within the Deadwood Formation, paleontological and paleoecological studies have been limited to the meager occurrences of trilobites and inarticulate brachiopods (Lochman-Balk, 1964, 1970, 1971). Only one taxonomic study has dealt directly with the Deadwood–Aladdin trace fossils, and that was the designation of a new ichnogenus, *Ixalichnus*, by Callison (1970). Consequently, this present work addresses not only the systematic ichnology, but also the paleoenvironmental and paleoecological aspects of the Deadwood–Aladdin ichnofauna.

The institutional abbreviation used in text is KSU, Kent State University, Kent, Ohio.

Regional Paleogeography

Throughout most of the Late Cambrian and Early Ordovician, two major facies belts developed across the cratonic shelf (Palmer, 1960; Fig. 2). In the region of the Black Hills, the Deadwood Formation and Aladdin Sandstone were deposited within the inner detrital belt, representing marginal–marine deposition. The transcontinental arch was the dominant tectonic element during much of the Paleozoic, and greatly influenced the type and distribution of the Deadwood–Aladdin deposystems (Lochman-Balk and Wilson, 1967). As with many deposits of this time, initial submergence of the Cambrian shelf in the Black Hills area occurred on Precambrian basement composed principally of schists and metaquartzites. Topographic relief on the basement surface consisted of metaquartzite monadnocks averaging no more than 30 m high. During the initial marine transgression into the Black Hills region these monadnocks became sources of metaquartzite boulders deposited as the basal conglomerate of the Deadwood Formation (Lochman-Balk and Wilson, 1967). Continued encroachment of the Cambro–Ordovician seas eastward was largely impeded by the transcontinental arch, which also supplied most of the terrigenous sediment of the inner detrital belt. The Black Hills area also was undergoing continual epeirogenic uplift throughout the Paleozoic, and may have represented a distal arm of the transcontinental arch (Gries, 1975).

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Fig. 1.—Generalized geologic map of the northern Black Hills in western South Dakota and eastern Wyoming. Outcrop pattern of the Deadwood Formation and Aladdin Sandstone shown as black band bounded by Precambrian basement and Lower Paleozoic carbonates. Location of measured sections are indicated by the white circles, and township and range coordinates for sections are given in lower left of this figure.

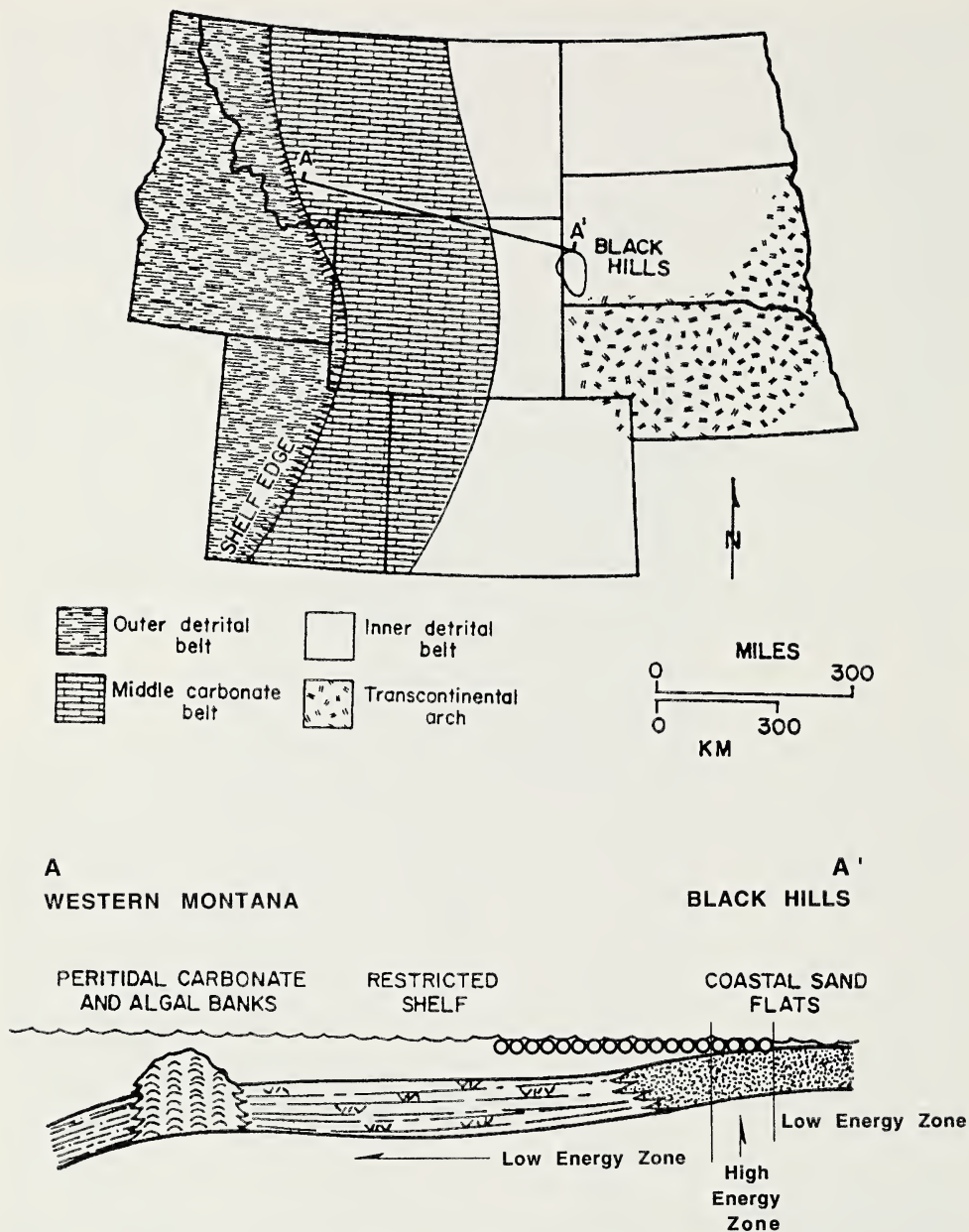


Fig. 2.—Paleogeographic map of the Cambro-Ordovician craton showing relative positions of the shelf edge and transcontinental arch, and lateral distribution of major facies belts. Cross-section A-A' shows basic depositional environments across the cratonic shelf, superimposed with Irwin's (1965) model of epeiric sedimentation, and distribution of energy zones in nearshore cratonic settings. The high energy zone in Irwin's (1965) model corresponds to lithofacies 2 and 4 of the Deadwood Formation and Aladdin Sandstone. Small circles on cross section represent zone of effective wave base. Diagram modified from Palmer (1960) and Sepkoski (1982).

Continual epeirogenic upwarping is suggested by a general thinning of Paleozoic strata as they onlap the Black Hills region (Gries, 1975; Lisenbee, 1975). Farther to the west, rocks characteristic of nearshore coastal deposystems of the Deadwood Formation grade into restricted subtidal-shelf deposystems of the middle carbonate belt, represented by Deadwood time-equivalent units of the Du Noir and Emerson formations of Wyoming and Montana (Miller, 1936; Sepkoski, 1982; Fig. 2). Both formations are composed of thick shale and intraclastic limestone sequences, lithologically similar to the middle parts of the Deadwood Formation (Fig. 3), and indicate that shelf-like conditions extended into the Black Hills during times of maximum transgression. However, open-ocean circulation across the shelf was restricted by algal buildups along the shelf margin (Sepkoski, 1982; Fig. 2). West of the algal banks, restricted shelf sedimentation of the middle carbonate belt abruptly grades into outer-shelf and shelf-slope sedimentation of the outer detrital belt (Palmer, 1960).

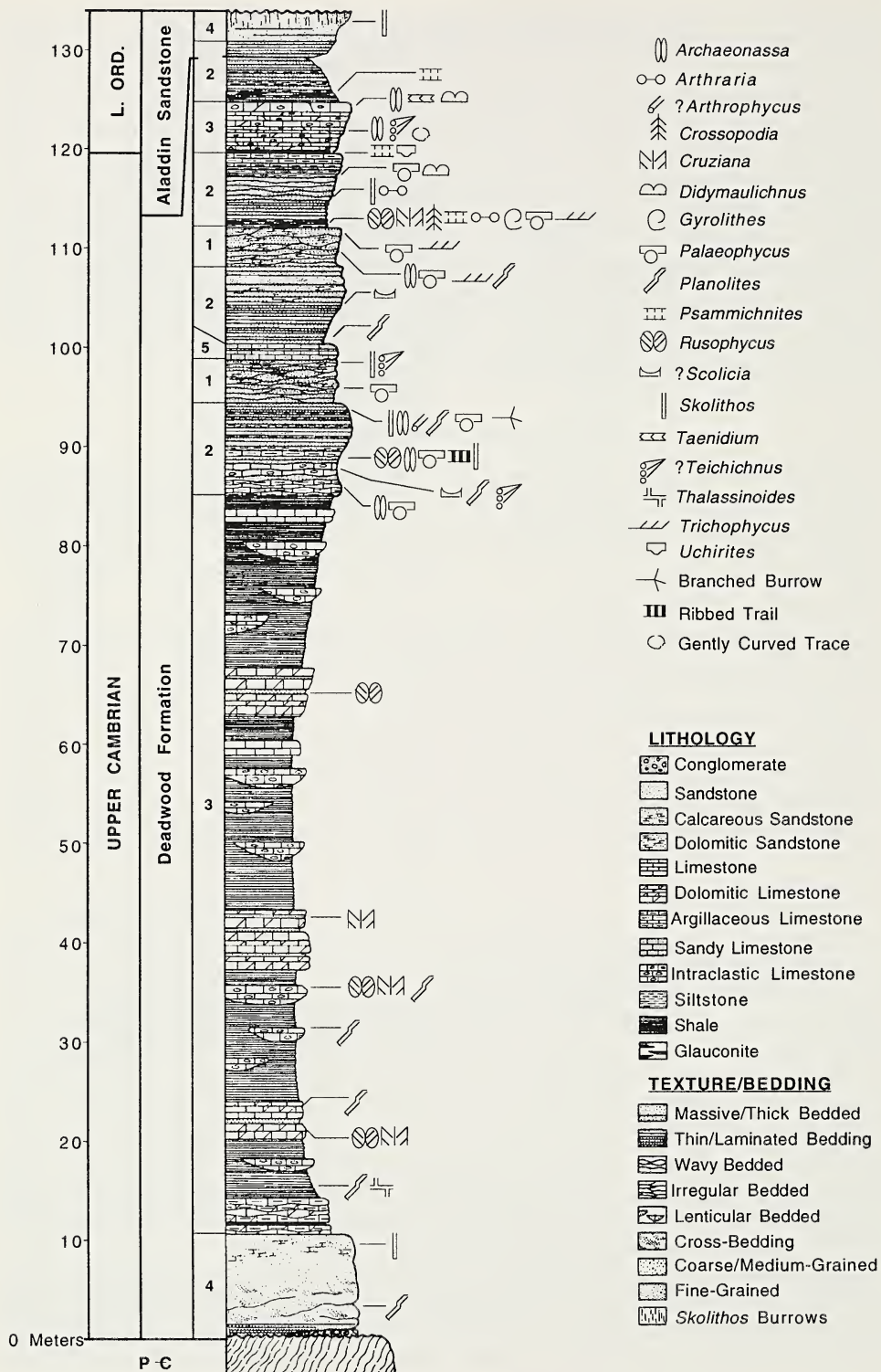
Deadwood and Aladdin Lithofacies

In the northern Black Hills (Fig. 1), five lithofacies were deposited throughout Cambro-Ordovician time in this region. These are: 1) irregularly bedded hematitic sandstones, 2) interbedded sandstone and siltstones, 3) interbedded shale and intraclastic limestones, 4) crossbedded sandstones, and 5) hematitic sandy limestones (Fig. 3, 4; Table 1).

Irregularly Bedded Hematitic Sandstone Lithofacies (Lithofacies 1).—Lithofacies 1 is characterized by dark reddish brown, medium-grained sandstone, with minor reddish green shale partings at the base. Bedding thickness is highly variable and irregular, ranging from thin-bedded (3–5 cm) to thick-bedded (25–66 cm) intervals. Bed thickness increases toward the top of the lithofacies. Primary sedimentary structures are rare within thick-bedded strata, but consist of multi-directional ripple marks and small-scale crossbed sets in the thin-bedded intervals. Glauconite is a minor constituent of the sandstone although hematite is rather abundant, giving the facies its characteristic red color. Dolomite and calcite alternate as the main cements, with calcite being predominant in the basal parts of the lithofacies.

Interbedded Sandstone and Siltstone Lithofacies (Lithofacies 2).—Lithofacies 2 is composed predominantly of light-colored, interbedded fine-grained sandstone and siltstone beds that are 0.5–2.0 cm thick. Current laminations, wavy crossbedding showing multiple current directions, parting lineations (Fig. 7D), and current-rippled bedding surfaces are common. Mudcracked surfaces also occur on some of the siltstone beds. Subordinate lithologies include shale as thin partings and clay drapes between sandstone and siltstone beds, which produced a flaser bedding texture, and fine-crystalline argillaceous limestone intervals normally found in the basal and upper parts of the lithofacies. Distinct grains or lenticular patches of glauconite are common within the sandstones and siltstones. Calcite is the dominant cement throughout. This facies represents the best exposed and most easily recognizable lithotype of the Deadwood Formation, and totally incorporates the lower 2.4 m of the overlying Aladdin Sandstone (Fig. 3).

Interbedded Shale and Intraclastic Limestone Lithofacies (Lithofacies 3).—Lithofacies 3 is composed of thin-bedded (3–10 cm), lenticular intraclastic limestone interbedded with thick (1–7 m) intervals of fissile shale, and thin-bedded (1–30 cm), finely crystalline to micritic limestone. Intraclasts are normally oblate



to tabular in shape, and set within a fine-grained crystalline or micritic limestone matrix. No current orientation of the intraclasts was evident. Upper surfaces of the intraclastic limestones commonly were cracked, pitted, and accompanied by protrusion of intraclasts above the bedding surface, suggesting possible hard-ground or firmground development from early subaqueous cementation (Leeder, 1982:291), or from exposure of partially lithified sediments from periodic storm erosion (Bromley, 1990:19). Lower contacts of intraclastic limestones were curved or appeared erosive into the underlying shale lithologies. Shale intervals are composed of gray, black, green, and sometimes purple calcareous fissile (1–4 mm thick) shale, along with subordinate amounts of lenticular-bedded calcareous siltstone.

Crossbedded Sandstone Lithofacies (Lithofacies 4).—Lithofacies 4 is composed of a basal trough crossbedded sandstone and conglomerate facies deposited in a high-energy, nearshore beach or barrier island system, that encompasses the basal 10 m of the Deadwood Formation, and supports a meager and poorly preserved trace-fossil assemblage consisting of *Skolithos* and scant *Planolites*(?) burrows. This lithofacies also characterizes the upper 1.5–2 m of the Aladdin Sandstone, which exhibits the typical *Skolithos* ichnofabric of lower Paleozoic orthoquartzites (Droser, 1991; Droser and Bottjer, 1993). Because of the density of the *Skolithos* burrows, this upper part of the Aladdin has an average ichnofabric index of 4 based on Droser and Bottjer (1993). Both the sedimentological and ichnological nature of lithofacies 4 support a high-energy interpretation for this lithofacies (Droser and Bottjer, 1989; Bockelie, 1991; Droser, 1991).

Hematitic Sandy Limestone Lithofacies (Lithofacies 5).—Lithofacies 5 is composed of a wavy bedded, very argillaceous to sandy, hematitic, crystalline limestone that contains no trace fossils. Laterally, this lithofacies is discontinuous, but is always associated with lithofacies 1 or 2, and is interpreted to have formed on an intertidal carbonate flat in areas undergoing relatively low siliciclastic influx (Fig. 4).

Because of the importance of their enclosed trace fossils, only lithofacies 1, 2, and 3 will be discussed in detail in the following sections. All three of these main lithofacies types fall within the typical Seilacherian, marine softground ichnofacies (Bromley, 1990:215; Bromley and Asgaard, 1991).

SYSTEMATIC ICNOLOGY

Of the 18 formally designated ichnogenera and 27 ichnospecies collected from the Deadwood and Aladdin formations, ten ichnogenera are diagnostic for paleoenvironmental interpretations due to their restricted occurrences (Fig. 3, 16; Table 1). Ichnotaxa important in paleoenvironmental interpretations include *Archaeonassa*, *Skolithos*, *?Scolicia*, *Gyrolithes*, and *Arthraria* in differentiating outer sand-flat environments from inner sand flats and the subtidal shelf. The presence of certain ichnospecies, such as *Planolites beverleyensis* and *Palaeophycus tubularis*, can also aid in differentiating the inner sand flats from the outer sand flats.

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Fig. 3.—Composite weathered profile of the Deadwood Formation and Aladdin Sandstone showing lithofacies and stratigraphic distribution of the collected trace fossils. Numbers to left of section correspond to lithofacies types described in text.



Ichnogenera such as *Cruziana*, *Rusophycus*, *Crossopodia*, and *Didymaulichnus* are more indicative of the subtidal shelf environments.

Ichnogenus *Archaeonassa* Fenton and Fenton, 1937
Archaeonassa fossulata Fenton and Fenton, 1937
 (Fig. 5A–C)

Material Examined.—*Archaeonassa fossulata* is one of the most common traces collected, being found at all three measured sections. Only two are illustrated showing the range in both morphology and preservation. A large slab (KSU 4556) with over ten individuals was collected at the Deadwood type locality. KSU 4597 was collected at the Little Elk Creek locality.

Description.—Straight to gently curving, trace preserved in concave epirelief; width 2–5 mm, maximum length 110 mm; trace consists of a smooth to transversely striated groove, bounded by variably defined lateral ridges; groove typically three-fourths total trace width, semicircular in cross section; bounding ridges smooth, ranging from sharp-crested to broadly-rounded semicircles in cross section; ridges are as high as groove is deep; trace may tangentially intersect shallow, circular depression averaging 15 mm in diameter and no more than 5 mm deep.

Discussion.—A much needed taxonomic review of *Archaeonassa* has been done by Buckman (1994). The Deadwood forms conform to two of Buckman's preservational variates, the smooth and standard type, of *A. fossulata* (Buckman, 1994:188, text-fig. 5A, B2), with the smooth variate being the more common of the two forms. The ichnogenus has been attributed to the locomotor activities of gastropods, trilobites, and even irregular echinoids (Fenton and Fenton, 1931, 1937; Buckman, 1994). Concerning the Deadwood material, echinoids may be excluded as potential trace makers, because they did not evolve until the Late Ordovician. Although trilobites cannot be entirely excluded as possible excavators of the Deadwood *Archaeonassa*, they seem unlikely given that *A. fossulata* is a true epirelief trace in construction (Buckman, 1994). Trilobite repichnion, such as *Cruziana*, are rarely preserved as epireliefs (Seilacher, 1970; Goldring, 1985). Gastropods seem to be the best candidates as trace makers, based on observations of trails left by the Recent snails *Littorina* and *Ilyanassa* on intertidal and subtidal flats in Washington and California (Fenton and Fenton, 1931, 1937). Important to this interpretation is that the Recent snails would occasionally excavate a small circular depression, terminating the epichnial groove. The Deadwood specimens of *Archaeonassa* imply a similar behavior as some of the trails terminate at shallow burrows (Fig. 5B), and continue on the reverse side of the bed (Fig. 5C). Similar epichnial grooves associated with circular depressions have been described as "annelid trails" by Hall (1852:pl. 14, fig. 3). These forms have subsequently been assigned to *A. fossulata* by Buckman (1994). If Hall's specimens from the Silurian of New York are truly conichnogenic with the Deadwood forms of *Archaeonassa*, then both represent the only recorded specimens exhibiting this particular behavior in the ichnogenus. All previously recorded occurrences of *Archaeonassa* were collected from intertidal deposits (Buckman, 1992,

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Fig. 4.—Cross section from the Little Elk Creek section in the east to the Bridal Veil Falls section in the west, illustrating vertical and lateral distribution of Deadwood Formation and Aladdin Sandstone paleoenvironments, along with corresponding Seilacherian, marine soft-ground ichnofacies. Horizontal line ("T") represents hypothetical time line used in Figure 16.

Table 1.—Summary of major lithofacies, associated trace fossils, and interpreted environments of deposition of the Deadwood Formation and Aladdin Sandstone. Under the column headed by "Trace Fossil Assemblages," D. T. = Dominant Trace, and S. T. = Subordinate Trace. Ethological interpretations of trace fossils from Frey and Pemberton (1984, 1985).

Lithofacies	Lithology	Primary sedimentary structures	Trace fossil assemblage	Environment of deposition
Lithofacies 1: Irregularly bedded hematitic sandstone.	Dolomitic-calcareous, ferruginous, fine- to medium-grained sandstone, with minor shale partings.	Multidirectional ripples Herringbone crossbedding Hummocky bedding Minor flaser bedding Mudcracks	D. T.: Fodinichnion of <i>Planolites</i> . S. T.: Fodinichnion of <i>Teichichnus</i> and <i>Trichophycus</i> . Domicnion of <i>Skolithos</i> and <i>Palaephycus</i> . Repichnion of <i>Archaeonassa</i> .	Inner sand flat Low energy, variable salinity, subaerial exposure
Lithofacies 2: Interbedded sandstone and siltstone.	Calcareous, glauconitic, fine-grained sandstone. Calcareous, glauconitic siltstone, with thin shale partings. Finely crystalline, argillaceous limestone.	Flaser-wavy bedding Multidirectional ripplemarks Herringbone crossbedding Parting lineations Mudcracks	D. T.: Repichnion of <i>Archaeonassa</i> and <i>Scolicia</i> . Domicnion of <i>Palaephycus</i> , <i>Skolithos</i> , and <i>Arthraria</i> . Fodinichnion of <i>Gyrolithes</i> and <i>Planolites</i> . S. T.: Cubichnion of <i>Rusophycus</i> . <i>Repichnion of Cruziana</i> and "Ribbed Trail." Fodinichnion of <i>Teichichnus</i> , <i>Arthropycus</i> , <i>Trichophycus</i> , <i>Psammichnites</i> , and "Branched Burrow."	Outer sand flats Moderate energy, high energy near low-tide line, subaerial exposure
Lithofacies 3: Interbedded shale and intraclastic limestone.	Multicolored, calcareous, fissile shale. Dark gray, finely crystalline limestones. Lenticular intraclastic limestones.	Strong fissility of shale Chaotic orientation of intraclasts Hardground development	D. T.: Cubichnion of <i>Rusophycus</i> . Repichnion of <i>Cruziana</i> and <i>Didymaulichnus</i> . Fodinichnion of <i>Psammichnites</i> and <i>Crossopodia</i> . S. T.: Repichnion of <i>Archaeonassa</i> . Fodinichnion of <i>Thalassinoides</i> , <i>Planolites</i> , <i>Taenidium</i> , and "Gently Curved Trace."	Restricted subtidal shelf Slow sedimentation with periodic tempestite deposition

Table 1.—Continued.

Lithofacies	Lithology	Primary sedimentary structures	Trace fossil assemblage	Environment of deposition
Lithofacies 4: Crossbedded sandstone.	Medium- to coarse-grained calcareous sandstones. Thick to massive, coarse-grained hematitic, dolomitic sandstones. Metaquartzite conglomerate at base of facies.	Large-scale trough crossbeds Large-scale tabular crossbeds Parting lineations	D. T.: Dominichion of <i>Skolithos</i> . S. T.: Fodinichion of <i>?Planolites</i> .	High energy beach Shifting substrate, well aerated
Lithofacies 5: Hematitic sandy limestone.	Very argillaceous, sandy, hematitic fine- to medium-crystalline limestone, and dolomitic limestone.	Wavy bedding Laterally discontinuous Associated with lithofacies 1 and 2	No trace fossils found.	Carbonate flat?



Fig. 5.—A–C. *Archaeonassa fossulata* Fenton and Fenton. A. Note pronounced lateral ridges bounding smooth medial groove, KSU 4597, concave epirelief, lithofacies 2, Little Elk Creek section. B. KSU 4556; note that trail terminates at a shallow burrow, concave epirelief, lithofacies 2, Deadwood type section. C. Reverse side of KSU 4556 illustrating exit trail, convex hyporelief. D, E. *Arthraria antiquata* Billings, both specimens figured occur in convex hyporelief from lithofacies 2, Bridal Veil Falls section. D. KSU 4539. E. KSU 4548. F. ?*Arthropycus* ichnospecies, KSU 4590, lithofacies 2, Little Elk Creek section. Bar scales in Fig. A–C and D represent 1 cm; bar scales in Fig. E and F represent 5 mm.

1994). All but two of the Deadwood specimens of *A. fossulata* were collected from lithofacies 1 and 2, which are interpreted as forming under intertidal conditions. This suggests that *Archaeonassa* may be an indicator of these environments.

Facies.—At the Deadwood type locality: KSU 4556 was collected at the top, while other specimens were collected at 0.3, 2.7, 4.5, and 6.5 m above the base of lithofacies 2; one specimen was collected 3.5 m above the base and two specimens were collected 2.5 m above the base of lithofacies 1. At Little Elk Creek: KSU 4597 was collected 0.5 m above the base of lithofacies 2. At Bridal Veil Falls: two specimens were collected 1.8 m above the base of lithofacies 3.

Ichnogenus *Arthraria* Billings, 1872

Arthraria antiquata Billings, 1872

(Fig. 5D, E)

Material Examined.—All specimens were collected from the Bridal Veil Falls locality, which include repositied specimens KSU 4537, 4539, 4540, 4542, 4545, and 4548.

Description.—Small dumbbell- to femur-shaped traces preserved in convex hyporelief; averaging 5–10 mm long, but can be up to 15 mm long; trace consists of two bulbous terminations of varying shape and size, connected by a shallow ridge; bulbous terminations range from 4–6 mm in diameter, and are usually 1–2 mm higher than the connecting ridge in transverse profile; shape of terminations vary on individuals; ranging from spherical, arrow-shaped to heart-shaped; surface of connecting ridge may have fine longitudinal striations; sectioning of trace revealed no vertical component to bulbous terminations or retrusive spreiten extending into bedding.

Discussion.—The absence of vertical shafts extending from the bulbous terminations, or retrusive or protrusive spreite between the terminations differentiates *Arthraria* from *Bifungites* and *Diplocraterion* (Fillion and Pickerill, 1984). In their taxonomic reevaluation of *Arthraria*, Fillion and Pickerill (1984) noted that all of their specimens from Bell Island were collected from shallow, intertidal to subtidal flat and lagoonal deposits. All of the Deadwood specimens were collected from lithofacies 2, which is interpreted as forming within the outer intertidal zone (Fig. 16; Table 1). This suggests that *Arthraria*, like *Archaeonassa*, may be used as an indicator of these environments of deposition.

Facies.—KSU 4542 and 4548 were collected 1.5 m above the base of lithofacies 2. The remaining specimens were collected at the base of lithofacies 2.

Ichnogenus *Arthropycus* Hall, 1852

? *Arthropycus* ichnospecies

(Fig. 5F)

Material Examined.—A single specimen (KSU 4590) was collected from the Little Elk Creek section. There were numerous specimens observed along the underside of large slabs at the Deadwood type section, but none were collectable.

Description.—Convex hyporelief, weakly bilobed burrow oriented horizontal to bedding; burrow diameter 15 mm, incomplete length of 39 mm; ornamentation consists of poorly developed, transverse annulations giving burrow surface a corrugated appearance; annuli occur as six alternating shallow furrows and ridges, each averaging 5 mm wide in longitudinal direction. Internal structure of burrow consists of obliquely oriented retrusive spreite; spreite ranging from 2–5 mm thick, sloping at 20–30° to bottom of burrow. In transverse section burrow cross section quadrate; height, 12 mm above bedding; retrusive spreite oriented concave-up, appearing as staked gutters; composition of spreite consisting of a fine-grained clastic material texturally different than host matrix.

Discussion.—Because of the incompleteness of this burrow only a tentative assignment to *Arthropycus* can be made. Typically, this ichnogenus exhibits branching morphology similar to *Phycodes* (Hall, 1952; Osgood, 1970; Häntzschel, 1975:W39, pl. 25, fig. 4). Similarities between this specimen and *Arthropycus* include the quadrate profile, weak bilobed morphology, and corrugated appearance of the burrow surface. The bilobed morphology coupled with the delicate transverse annulations help distinguish *Arthropycus* from *Phycodes*, and similar spreite-bearing ichnogenera like *Teichichnus* (Osgood, 1970). The orientation of the spreite in the burrow, combined with the infilling material being texturally different from the host rock indicates that *Arthropycus* was actively infilled by the trace maker.

Facies.—The specimen was collected 4.5 m above the base of lithofacies 2. Specimens observed in the field were all from beds pertaining to lithofacies 2.

Ichnogenus *Crossopodia* M'Coy, 1851

Crossopodia ichnospecies

(Fig. 6A, B)

Material Examined.—Two specimens on a single slab (KSU 4542) and a single specimen (KSU 4544) were collected from the Bridal Veil Falls section.

Description.—Straight to gently curving, longer than wide, distinctly bilobed trace preserved in concave and convex epireliefs; trace width between 5–10 mm, not constant along full length of trace due to undulating lateral margins; lobes covered by coarse striae, grouped five to seven striae per centimeter, angled 20° to midline; striae represent external expression of backfill menisci, and give lateral margins a ropy texture and trace a feather-like appearance; composition of menisci same as host matrix; lobes separated by a 1–2 mm-thick median groove in convex epireliefs, or ridge in concave epireliefs; menisci do not extend into median area. In transverse section trace has low triangular profile where apex is flatly truncated by median groove.

Discussion.—The precise relationship between *Crossopodia* and other ichnogenera having similar morphologies needs examination. Several authors have suggested that *Crossopodia* is conichnogenetic with *Psammichnites* and even *Cruziana* (Eagar et al., 1985; Maples and Suttner, 1990). Unlike *Cruziana*, *Crossopodia* is a three-dimensional backfill trace, and although the concave epireliefs specimens of *Crossopodia* superficially resemble *Cruziana* (Fig. 6A), they actually represent the epichnial groove of a washed-out, full-relief form. *Psammichnites* is also morphologically similar to *Crossopodia*. Particularly when *Psammichnites* is preserved as convex epireliefs (compare Fig. 6B with 11A). However, the presence of a distinct but unstriated medial groove in *Crossopodia*, rather than a medial lobe as in *Psammichnites*, separates the two ichnogenera. The menisci of *Crossopodia* represent backfill structures, and are morphologically similar to ?*Crossopodia* from the Pennsylvanian Fountain Formation of Colorado (Maples and Suttner, 1990). The ?*Crossopodia* from the Fountain Formation has backfill menisci consisting of oriented mica flakes. This differentiates it from our specimens from the Deadwood Formation, where the menisci do not represent any textural or mineralogical difference from the hosting matrix. *Crossopodia* exhibits two distinct morphological types that may reflect gross behavioral or morphological differences in the trace makers. *Crossopodia* specimens from the Cretaceous have menisci bundles that are coarsely lobate and oriented at a transverse to oblique angle from the midline (Hattin and Frey, 1969). This type was interpreted to have formed from a nekto-benthonic organism, which would briefly alight on the sediment–water interface in constructing the trace before swimming off. Other

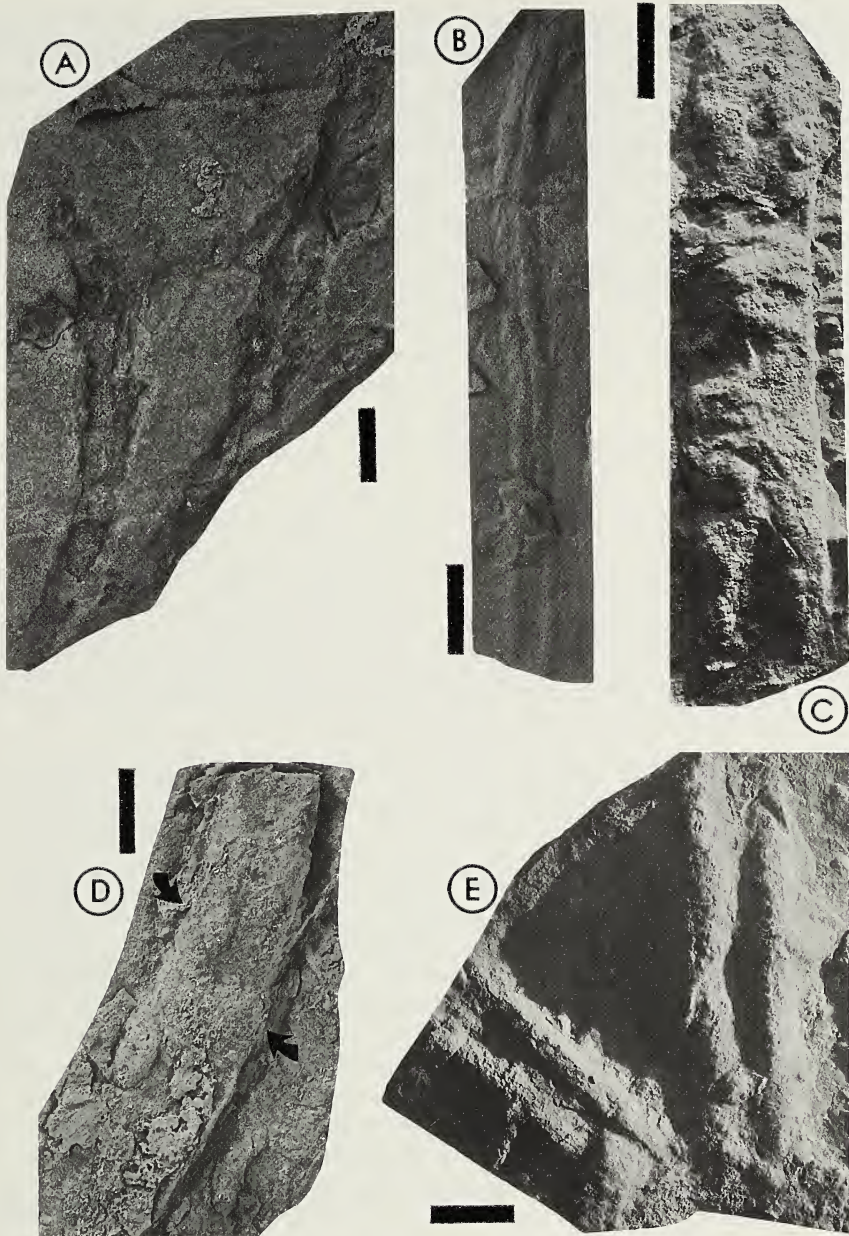


Fig. 6.—A, B. *Crossopodia* ichnospecies. A. KSU 4542, concave epirelief, lithofacies 2, Bridal Veil Falls section. B. KSU 4544, convex epirelief, lithofacies 3, Bridal Veil Falls section. C. *Cruziana* ichnospecies A, note distinct bilobed terminations that become poorly defined in middle of trace, also note coarse striations; KSU 4667, convex hyporelief, lithofacies 3, Little Elk Creek section. D. *Cruziana pudica* James, note faint *Rusophycus*-like swellings at arrows; KSU 4547, lithofacies 3, Bridal Veil Falls section. E. *Cruziana* ichnospecies B, KSU 4667, convex hyporelief, lithofacies 3, Little Elk Creek section. Bar scales represent 1 cm.

Crossopodia, such as specimens from the Upper Cambrian Deadwood Formation, the Pennsylvanian of Colorado (Maples and Suttner, 1990), the Upper Pennsylvanian of Kansas (Bandel, 1967), the Silurian of New York (Hall, 1852:pl. 13, fig. 1b), and the Ordovician of France (Häntzschel, 1975:pl. 34, fig. 2b), exhibit menisci bundles that are finer and oriented more acute to the midline of the trace. Most of these forms are interpreted to represent a more benthonic mode of life of the trace maker (Bandel, 1967). *Crossopodia* is restricted to the distal intertidal and subtidal lithofacies of the Deadwood Formation (Fig. 3, 10).

Facies.—KSU 4542 was collected 2 m above the base of lithofacies 2. KSU 4544 was collected 3.1 m above the base of lithofacies 3.

Ichnogenus *Cruziana* d'Orbigny, 1842

Cruziana pudica James, 1885

(Fig. 6D)

Material Examined.—Specimen KSU 4547 was collected at the Bridal Veil Falls location.

Description.—Longer than wide, weakly bilobed trace preserved in convex hyporelief; width variable, ranging from 12–14 mm, incomplete length 50 mm; height no more than 5 mm above bedding; trace composed of three individual *Rusophycus*-like swellings averaging 10 mm in length, and represent widest part of hypichnial ridge; swellings separated 20–40 mm in longitudinal direction by interlobate ridge; lobate swellings and interlobate areas divided medially by faint groove; groove 1–2 mm wide, and no more than 0.5 mm deep; lobe and interlobe surfaces ornamented with poorly preserved, oblique striae angled 60–70° from the midline, grouped five to six striae per centimeter; striae parallel to each other near midline, diverge and converge at lateral margins. In transverse section, trace cross section quadrate, with greatest height at *Rusophycus* swellings.

Discussion.—The assessment of this *Cruziana* to *C. pudica* is based on the ethological intergradation between *Cruziana* and *Rusophycus* observed in this ichnospecies (Osgood, 1970; Pickerill, 1977). The figured specimen shows an interconnected series of *Rusophycus*-like swellings (arrows in Fig. 6D), indicating that the trace maker vertically excavated into the substrate, then moved forward for a short distance before repeating the procedure. This intergradation in ethological types is seen in the Deadwood material and in specimens from the Ordovician of Ohio and Wales (Osgood, 1970; Pickerill, 1977). Other similarities between the Deadwood and Ordovician specimens are the presence of a weak median groove and poorly developed striated lobe surfaces. Because of the dual ethological nature exhibited in this ichnospecies, various authors have classified it as both *Rusophycus* (Hall, 1852; Osgood, 1970) and *Cruziana* (James, 1885; Seilacher, 1970; Pickerill, 1977). Because the predominant component of movement is lateral rather than vertical, we are inclined to agree with Pickerill's (1977) classification of the ichnospecies under *Cruziana*.

Facies.—This specimen was collected 1.5 m above the base of lithofacies 3.

Cruziana ichnospecies A

(Fig. 6C)

Material Examined.—A single specimen (KSU 4667) was collected on a large slab from the Little Elk Creek locality.

Description.—Poorly developed bilobed trace preserved in convex hyporelief; width 12 mm, length 65 mm, height 3 mm above bedding; lobes well developed at ends, become indistinct medially; where developed, lobes 5–6 mm wide, tapering to 3 mm wide at ends; covered with coarse striae that give trace a corrugated appearance; striae 1–1.5 mm thick, grouped three to four striae per centimeter,

oriented at 60–70° from midline. In transverse section trace has semicircular cross section where lobes are well developed, becoming quadrate where individual lobes are ill defined.

Discussion.—Unlike typical *Cruziana*, this specimen does not show complete bilobed morphology along its entire length. This characteristic may have been due to postconstruction erosion that washed out the epichnial furrow, or represents a behavioral variation of *Cruziana*. Close examination of the specimen revealed no preservational irregularities or scouring. This observation was reinforced by the lack of abrasion or scouring of other traces on the same slab. Consequently, the weak bilobate morphology coupled with coarse, transversely directed striae probably represent a behavioral variate with the trilobite having a procline, or head-down attitude during trace construction (Seilacher, 1970:452, fig. 4).

Facies.—This specimen was collected 29 m above the base of lithofacies 3.

Cruziana ichnospecies B (Fig. 6E)

Material Examined.—Two specimens were collected on a single slab (KSU 4667) along with *Cruziana* ichnospecies A from the Little Elk Creek locality.

Description.—Longer than wide, distinctly bilobed trace preserved in convex hyporelief; width from 12–16 mm, length from 28–45 mm, height from 2–6 mm above bedding; lobes typically one-third total width of trace; 3–4 mm wide in small specimen, 6–8 mm wide in large specimen; lobes separated by distinct medial groove that is one-third total trace width, and 2 mm deep; groove expands at trace terminations forming distinct V-shaped gap between lobes, gap more prominent in smaller forms. Medially, lobes ornamented with very short, transversely oriented striae ranging from 0.5–2 mm thick, grouped eight to nine striae per centimeter; medial striae better developed in large forms. Laterally, lobes have fine, longitudinally-directed striations running parallel to trace margins; lateral striae better developed in smaller forms. In transverse section, trace has triangular cross section, while individual lobes are quadrate-shaped, with steep-sided lateral margins; highest part of trace at interior margin of lobes adjacent to median groove, with trace gently tapering to bedding anteroposteriorly and laterally.

Discussion.—The dual set of striae, with one on the exterior and the other on the interior parts of the lobes, is typical of Cambro–Ordovician *Cruziana* (Seilacher, 1970:449–452, fig. 3). The interior, oblique striae probably were constructed by movement of the trilobite endopodites that facilitated locomotion of the organism through the sediment. The longitudinal striae along the lobes' outer margins were likely produced by the expodites or gill structures being dragged as the animal moved forward.

Facies.—These specimens were collected 29 m above the base of lithofacies 3.

Cruziana ichnospecies C (Fig. 7A)

Material Examined.—A single specimen (KSU 4600) was collected from the Little Elk Creek section.

Description.—Longer than wide, strongly bilobed trace preserved in convex hyporelief; width 13 mm, length 30 mm, height 4 mm above bedding. Lobes approximately one-half total width, separated by a distinct, narrow median groove; groove 1.5 mm wide, 2–3 mm deep; lobes covered with fine and coarse striae; fine striae less than 0.5 mm thick, oriented at 70–75° from midline; coarse striae typically 1 mm thick, oriented at 25–45° from the midline; striations grouped at nine to 11 per centimeter; coarse striae typically cut fine striae. In transverse section lobes have semicircular cross section, with steep-sided lateral margins.

Discussion.—One feature of interest is that this trace appears to merge into a highly bioturbated region that resembles a poorly defined *Rusophycus*.



Fig. 7.—A. *Cruziana* ichnospecies C on left merging with a *Rusophycus*-like trace on right of figure, also note crosscutting of trace by ?*Planolites* burrows; KSU 4600, convex hyporelief, lithofacies 3, Little Elk Creek section. B–D. *Didymaulichnus lyelli* (Rouault). B, C. Both specimens occur on same slab; KSU 4525, convex hyporelief, lithofacies 3, Bridal Veil Falls section. D. Slab with *D. lyelli* (represented by letter “D”), note morphological shift from a bilobed hypichnia (top of trail) to a single ridge structure (bottom of trail); also on same slab are *Planolites beverleyensis* (represented by letter “P”), and *Skolithos* ichnospecies (represented by letter “S”); narrow striations and ridges oriented from left to right on slab represent parting lineations; KSU 4676, convex hyporelief, lithofacies 2, Deadwood type section. Bar scales represent 1 cm.

Facies.—This single specimen was collected 8 m above the base of lithofacies 3.

Ichnogenus *Didymaulichnus* Young, 1972

Didymaulichnus lyelli (Rouault, 1850)

(Fig. 7B–D)

Material Examined.—Two specimens occur on a single slab (KSU 4525) collected at the Bridal Veil Falls locality. A single specimen (KSU 4676) was collected at the Deadwood type locality.

Description.—Trace smooth, unornamented, bilobed over most of trace length, but may merge into single ridge structure, preserved in convex hyporelief; trace varies from 3–5 mm wide when bilobed, about half this width when occurring as a single ridge; length incomplete; lobes typically separated by narrow, well-developed median groove that is one-fifth total width of trace; groove about one-half as deep as lobes are high; lateral margins undulatory. In transverse section lobes have semicircular cross section.

Discussion.—The Deadwood forms of *D. lyelli* closely resemble, both in size and shape, specimens from the Ordovician of Portugal (Häntzschel, 1975:W61) and from the Upper Cretaceous Cardiff Formation of Alberta (Vossler et al., 1989). Particularly, all illustrated forms of *D. lyelli* exhibit transverse undulations along the lateral margins of the trace. Various trace makers and ethological interpretations have been suggested for *Didymaulichnus*, ranging from arthropods, gastropods, and worms (Glaessner, 1969; Young, 1972). On the basis of the morphological shift from a bilobed to single ridge repichnion (Fig. 7D), however, the Deadwood specimens probably represent locomotion of gastropods (Stanley, 1984; Vossler et al., 1989). For the purposes of this paper, *D. lyelli* is tentatively classified as a repichnion based on the unmeandering disposition of the ichnogenus and lack of evidence for active fill. Other than the occurrence of *D. lyelli* in the Cardiff Formation, which is interpreted as a normal marine shelf deposit, all other reported occurrences of the ichnospecies have been from marginal–marine to very nearshore deposits (Eager et al., 1985; Hakes, 1985). This may suggest that at least Early Paleozoic forms of this ichnospecies indicate these depositional regimes.

Facies.—KSU 4525 was collected 4.8 m above the base of lithofacies 3. KSU 4676 was collected 6.5 m above the base of lithofacies 2.

Ichnogenus *Gyrolithes* de Saporta, 1884

Gyrolithes polonicus Fedonkin, 1980

(Fig. 8A, B, D)

Material Examined.—Numerous specimens collected on two large slabs (KSU 4526, KSU 4530) at the Bridal Veil Falls locality.

Description.—Semicircular to semi-ovoid trace in plan view, with spiral vertical component in transverse view, preserved in full relief, concave hyporelief, or concave epirelief; epireliefs represent washed-out full-relief structures; diameter of trace ranges from 14–30 mm; concave epirelief forms (Fig. 8A) consisting of annulated U-shaped groove flanked by narrow lateral ridges; groove may be bisected by well-defined, narrow, median ridge; groove and median ridge ornamented with arcuate annulations; annuli average 1 mm thick, and are regularly spaced along trace length; full relief forms consist of structureless, infilled burrow with no ornamentation; infilling material appears same as host matrix; groove or full-relief burrow average 2.5–5 mm wide. In transverse section, trace corkscrews into host medium; vertical distance between each whirl varies from 3–5 mm.

Discussion.—Deadwood specimens of *G. polonicus* are similar in size and shape to those collected from the Lower Cambrian of Newfoundland (Crimes and



Fig. 8.—A, B, D. *Gyrolithes polonicus* Fedonkin. A. KSU 4530, illustrating median ridge and annulated trace margins, concave epirelief. B. Reverse side of KSU 4530, thickness of bed separating epichnial side from hypichnial side is 5 mm; concave hyporelief, lithofacies 2, Bridal Veil Falls section. D. Concave hyporelief cast of full-relief burrow; note faint annulations on burrow floor in specimen on left; KSU 4526B, lithofacies 2, Bridal Veil Falls section. C. *Palaeophycus alternatus* Pemberton and Frey, KSU 4546; convex hyporelief, lithofacies 2, Deadwood type section. E. *Palaeophycus crenulatus* Buckman, note burrow is crosscut by a *Skolithos* (labeled by letter "S"); KSU 4557, convex hyporelief, lithofacies 2, Deadwood type section. Bar scales represent 1 cm.

Anderson, 1985) and the Onega Platform of eastern Europe (Fedonkin, 1977). Typically this ichnospecies is characterized by a structureless, full-relief burrow that has a vertical, corkscrew behavior. However, some Deadwood forms of *G. polonicus* are unique in that the internal features of the burrow are evident (Fig. 8A, D), consisting of an annulated epichnial groove with a median ridge. The annulated interior of the burrow suggests a trace maker using peristaltic movement to construct the trace. Examination of the specimens preserved in full relief show that the infilled sediment is the same as the host material, suggesting the burrows were passively filled. *Gyrolithes polonicus* probably represents a fodinichnion, based on the elaborate geometry of the trace. As with *Arthraria antiquata* and *Archaeonassa fossulata*, *G. polonicus* appears to be restricted to the outer sand-flat facies (lithofacies 2), and could be an indicator of these environments of deposition (Fig. 16).

Facies.—All specimens were collected in the basal 1 m of lithofacies 2.

Ichnogenus *Palaeophycus* Hall, 1847
Palaeophycus alternatus Pemberton and Frey, 1982
(Fig. 8C)

Material Examined.—Two specimens on a single slab (KSU 4546) were collected at the Deadwood type section.

Description.—Straight to slightly curving burrow, oriented parallel to bedding, preserved in convex hyporelief or full relief; burrow diameters vary between 7–11 mm, not constant along burrow length; maximum burrow length is 80 mm; burrow thinly lined with fine-grained material similar to laminae of the host matrix; no collapse structures evident, but infilling material same as host material; burrow surface ornamented with alternating fine longitudinal striae and thick transverse annuli; striae thread-like, discontinuous but parallel to lateral margins of burrow; annuli occur as swellings along burrow wall, range 3–4 mm thick in longitudinal direction, average three to four annuli per centimeter; striae indistinct on annuli. In transverse section burrows extend 1–4 cm below bedding surface; burrow cross section ovoid to circular-shaped; oval burrows have long dimension parallel to bedding; no external or internal distortion of bedding laminae evident; upper contact of burrow with host matrix may be gradational.

Discussion.—The Deadwood specimens of *Palaeophycus alternatus* conform well to Pemberton and Frey's (1982) description. Typical of this ichnospecies is the alternating annulate and striate nature of the burrow wall, and general lack of internal collapse structure as noted in other ichnospecies of *Palaeophycus* (Pemberton and Frey, 1982; Buckman, 1995). However, in one specimen (burrow at top in Fig. 8C), the burrow shifts from a cylindrical to oval cross section along its length, which may indicate slight burrow collapse.

Facies.—*Palaeophycus alternatus* was collected 5 m above the base of lithofacies 2.

Palaeophycus crenulatus Buckman, 1995
(Fig. 8E)

Material Examined.—A single specimen (KSU 4557) was collected at the Deadwood type section.

Description.—Straight burrow preserved as convex hyporelief; diameter averages 15 mm; incomplete length of 35 mm; burrow distinctly lined with a fine-grained sand similar to host matrix; burrow lining with numerous, regularly spaced, transverse annuli; annuli range from 1–2 mm thick, average five annuli per centimeter. In transverse section burrow extends 4–6 cm below bedding surface; cross section oval, with long axis of ellipse parallel to bedding; collapse structure represented as concave-up laminae; internal composition of fill same as host matrix.

Discussion.—In his re-evaluation of *Palaeophycus*, Buckman (1995) noted that all annulated forms of *Palaeophycus* should be assigned to a new ichnospecies *P. crenulatus*, or to *P. alternatus*. This specimen from the Deadwood Formation conforms well with Buckman's (1995) description in that it has a distinct annulated lining but does not possess the longitudinal striations characteristic of *P. alternatus*. Differences between Buckman's (1995) figured specimens and our specimen do exist, however. *Palaeophycus crenulatus* from the Pennsylvanian Mullaghmore Sandstone of Ireland (Buckman, 1995:fig. 2A–D) exhibit finer annulations along the burrow wall that average one-half to one annulus per millimeter. The Deadwood specimen averages one annulus every two millimeters, with adjacent annuli being further apart. This variability in annulation does not warrant exclusion of the Deadwood burrow from *P. crenulatus*, and is probably due to the Deadwood form not having as tightly packed annuli as the European varieties. Other than the Carboniferous of Ireland (Buckman, 1995), *P. crenulatus* has only been recorded from the Jurassic of Greenland (Dam, 1990). This makes the Deadwood specimen the oldest assigned to this ichnospecies, and the only one reported from North America.

Facies.—This specimen was collected 3.5 m above the base of lithofacies 2.

Palaeophycus sulcatus (Miller and Dyer, 1878)
(Fig. 9A)

Material Examined.—Two specimens occur on a single slab (KSU 4586) collected at the Deadwood type locality.

Description.—Straight to gently curved burrow, oriented parallel to bedding, preserved in convex hyporelief; burrow diameters vary from 2–8 mm, remaining constant along burrow length; maximum length 50 mm. Burrow lining consisting of silt- to clay-sized material; sculptured with thin, irregular, longitudinal ridge and groove structures that give lining an anastomosing texture; ridges and grooves average 0.5 mm thick and range between 2–18 mm long. In transverse section, burrow cross section circular; height 0.5–5 mm above bedding; infilling material same as host matrix, with no collapse structure evident.

Discussion.—*Palaeophycus sulcatus* is differentiated from *P. alternatus* by the coarser striae and absence of annulations or swellings along the burrow wall (Pemberton and Frey, 1982; Buckman, 1995).

Facies.—Specimens were collected 5 m above the base of lithofacies 2.

Palaeophycus tubularis Hall, 1847
(Fig. 10A–C)

Material Examined.—*Palaeophycus tubularis* was identified in the field at all sections, most specimens occur on large slabs. Reposited material includes KSU 4566 and 4567 from the type locality.

Description.—Straight to gently curved, smooth, unornamented, thinly lined burrows preserved as convex hyporelief or full relief. Burrow diameters range from 3–20 mm, remaining constant along burrow length; lining consists of very fine-grained silt- or clay-sized material similar to shale partings of host bed. In transverse section burrow circular to oval in cross section; collapse structures and deformation laminae common in burrow interior; composition of fill same as host matrix; burrows occasionally exhibit gradational upper contacts with host bed.

Discussion.—*Palaeophycus tubularis* was collected from most of the Deadwood–Aladdin lithofacies, with the exception of lithofacies 3. Typical *P. tubularis* from lithofacies 1, which represents an environmentally stressful intertidal regime,

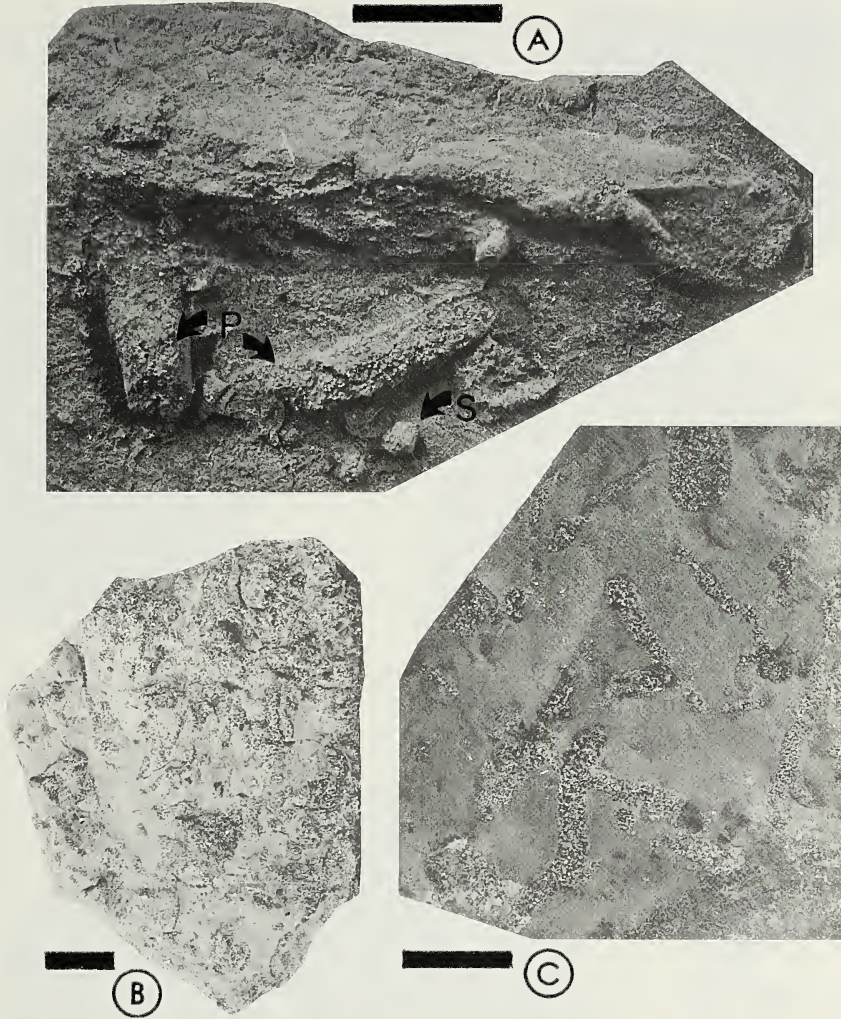


Fig. 9.—A. *Palaeophycus sulcatus* (Miller and Dyer), note association with *Planolites beverleyensis* (Billings) (represented by the letter “P”) and *Skolithos* ichnospecies preserved as knob-like fillings of the burrows (represented by the letter “S”); full relief and convex hyporelief, lithofacies 2, Deadwood type section. B, C. *Planolites montanus* Richter, both figures preserved in full relief, collected from lithofacies 2, Deadwood type section, note textural and chromatic differences between traces and host lithology indicating active fill of burrows. B. KSU 4577. C. KSU 4579. Bar scales represent 1 cm.

were in the size range of 3–10 mm in diameter, having an average diameter of 7 mm. Collected specimens of *P. tubularis* from lithofacies 2, which represents a more normal marine intertidal setting, fell in the size range of 12–20 mm, with an average burrow diameter of 15 mm. Given the stressful conditions of the inner sand flats, such as variable salinity and oxygen, there may be an ecological cause to the disparity in size of *P. tubularis*. Similar characteristics have been observed in intertidal mollusks from the Gulf of California (Fürsich and Flessa, 1987), and in Pennsylvanian marginal marine trace-fossil assemblages of Kansas (Hakes, 1985).



Fig. 10.—A–C. *Palaeophycus tubularis* Hall. A. Cross section of burrow figured in C, note concave-up laminae from collapsing of the burrow; KSU 4566, full relief, lithofacies 2, Deadwood type section. B. KSU 4567, full relief, lithofacies 2, Deadwood type section. C. Plan view of 9A, convex hyporelief to full relief, lithofacies 2, Deadwood type section. D. *Planolites beverleyensis* Billings, KSU 4523, full relief, lithofacies 2, Bridal Veil Falls section. Bar scales represent 1 cm.

Facies.—KSU 4566 and 4567 were collected 3.5 m above the base of lithofacies 2 at the type section. Other specimens from the type section were collected at 0.3, 5.0, and 6.5 m above the base of lithofacies 2, and at the base and 2.5 m above the base of lithofacies 1. At the Little Elk Creek section specimens were collected 4.5 m above the base of lithofacies 2 and 5.3 m above the base of lithofacies 1. At Bridal Veil Falls, specimens were collected at the base of lithofacies 2.

Ichnogenus *Planolites* Nicholson, 1873
Planolites beverleyensis Billings, 1862
(Fig. 7D, 9A, 10D)

Material Examined.—Numerous examples occur on single slabs (KSU 4586, 4558) collected at the Deadwood type section. Slab KSU 4523 was collected at the Bridal Veil Falls locality. Many specimens were also observed in the field at all of the measured sections, but were not collected.

Description.—Cylindrical, usually gently curved, sometimes straight, unlined burrows preserved in full relief; burrow diameters range from 7–12 mm, average 10 mm, remaining constant along burrow length in individuals; branching not evident, interruptions and crossovers common. Burrow fill structureless, consisting of a coarser-grained material than host matrix; burrows usually stand out on bedding due to discoloration of fill material. In transverse section burrows have circular cross section, and are oriented at various angles to bedding.

Discussion.—Deadwood representatives of *Planolites beverleyensis* appear slightly smaller than Pemberton and Frey's (1982) material. They are, however, 5–8 mm larger than *P. montanus* from the Deadwood, and have a less contorted burrow attitude. Generally, *Planolites* was collected from all lithofacies types, although it was more commonly found in lithofacies 1 and 2. Specifically, *P. beverleyensis* appears to be restricted to lithofacies 2.

Facies.—KSU 4586 and 4548 were collected 5.0 and 5.9 m above the base of lithofacies 2, respectively. KSU 4523 was collected 1.5 m above the base of lithofacies 2.

Planolites montanus Richter, 1937
(Fig. 9B, C)

Material Examined.—Specimens of *Planolites montanus* were observed and collected from all sections and lithofacies types. Specifically, KSU 4565, 4577, 4579, 4588, 4559, and 4569 represent slabs with numerous burrows collected from the Deadwood type section; KSU 4589, 4666, 4596, and 4675 were collected from the Little Elk Creek section.

Description.—Small, cylindrical, strongly curved to contorted, unlined burrows preserved in full relief. Burrow diameters vary from 1–4 mm, averaging 2.6 mm; diameter remaining constant in individuals. Sparsely populated bedding surfaces usually have curving burrows; burrows crowded on bedding surfaces are contorted. No branching evident, crossovers and burrow interruptions common. Burrow fill structureless; always coarser grained and having a different color than host matrix. In transverse section burrows have circular cross section, rarely oval; oriented at various attitudes to bedding.

Discussion.—*Planolites montanus* was found in all lithofacies of the Deadwood, but occurs in abundance in lithofacies 1. In their treatment of Lower Ordovician intertidal deposits in Argentina, Mángano et al. (in press) noted an extreme segregation in the taxonomic components of the trace-fossil assemblages.

High intertidal deposits contain only *P. montanus*. Other than the occurrence of a few *Palaeophycus* and *Trichophycus* ichnospecies, the inner sand-flat environments of the Deadwood Formation were dominated by *Planolites montanus*. This may suggest that in tidal-dominated, Lower Paleozoic siliciclastic sequences, monoichnospecific occurrences of *P. montanus* can be used to recognize high intertidal flat deposits.

Facies.—At the type section: KSU 4565 and 4577 were collected 3.5 m above the base of lithofacies 1; KSU 4579 and 4588 were collected 2.5 m, and KSU 4559 and 4569 were collected 5.9 m above the base of lithofacies 2. At the Little Elk Creek section: KSU 4675 was collected 3.5 m above the base of lithofacies 1; KSU 4589 was collected 3 m, and KSU 4666 was collected 9 m above the base of lithofacies 3.

Ichnogenus *Psammichnites* Torrel, 1870
Psammichnites ichnospecies
(Fig. 11A, C)

Material Examined.—One specimen occurs on a small slab (KSU 4534), and two specimens occur on a large slab (KSU 4535) collected from the Bridal Veil Falls locality.

Description.—Meandering to gently curved, longer than wide trace preserved in convex epirelief and full relief; width 5–11 mm; length variable, maximum 30 cm. Full-relief trace consists of a median lobe, laterally bounded by two platforms ranging from 3–4 mm wide; median lobe may be collapsed along parts of trace forming a groove; platforms bounded at lateral margins by narrow ridge structures averaging 1 mm wide; platforms horizontal to bedding; ridge and platform covered with fine, transverse ribbing indicative of backfill lamellae, and does not extend into median lobe; backfill material similar to host matrix; individual lamellae 0.8 mm thick, grouped seven to eight lamellae per centimeter. Specimens in epirelief poorly preserved (Fig. 11A); consisting of a single broad median lobe, bounded along lateral margins by a thin inner groove and outer ridge; ridge and groove with irregularly spaced striations oriented oblique to the midline of trace. In transverse section, burrows have an oval cross section, with the long axis of ellipse parallel to bedding.

Discussion.—Morphological differentiation between *Psammichnites* and *Scolicia* is based on the presence of a single ridge that symmetrically divides the backfilled string into two parts in the former ichnogenus (D'Alessandro and Bromley, 1987). *Scolicia* typically has two or more sediment strings. Backfill structures in *Psammichnites* are generally loosely packed compared to *Scolicia*. In the Deadwood forms this symmetrical ridge is represented by a broad lobe that does not exhibit transverse ribbing, suggesting loose packing of sediment by the trace maker. In their examination of the trace fossils from the lower Cambrian Ratcliffe Brook Formation in eastern Canada, Hofmann and Patel (1989:144, fig. 4a) illustrate *Psammichnites gigas* that look similar to our specimens from the Deadwood Formation. *Psammichnites gigas* consists of a medial lobe bounded laterally by narrow ridges. Hofmann and Patel (1989) also noted a similarity between their specimen of *P. gigas* and specimens of *Subphyllochora* ichnospecies from the Ratcliffe Brook Formation (Hofmann and Patel, 1989:fig. 2d, e) and *S. laevis* from the Cretaceous of the Carpathians of Poland (Ksiazkiewicz, 1970:290, 1977:134–135, pl. 16, fig. 1–3). However, the authors were tentative in their assessment of the Ratcliffe Brooks *Subphyllochora* and thought it may be a preservational variate of *Psammichnites* or *Scolicia*. As a taxonomic note, *Subphyllochora* has recently been synonymized as *Scolicia* by Uchman (1995), who considers *Subphyllochora* as the hypichnial expression of *Scolicia* (see dis-

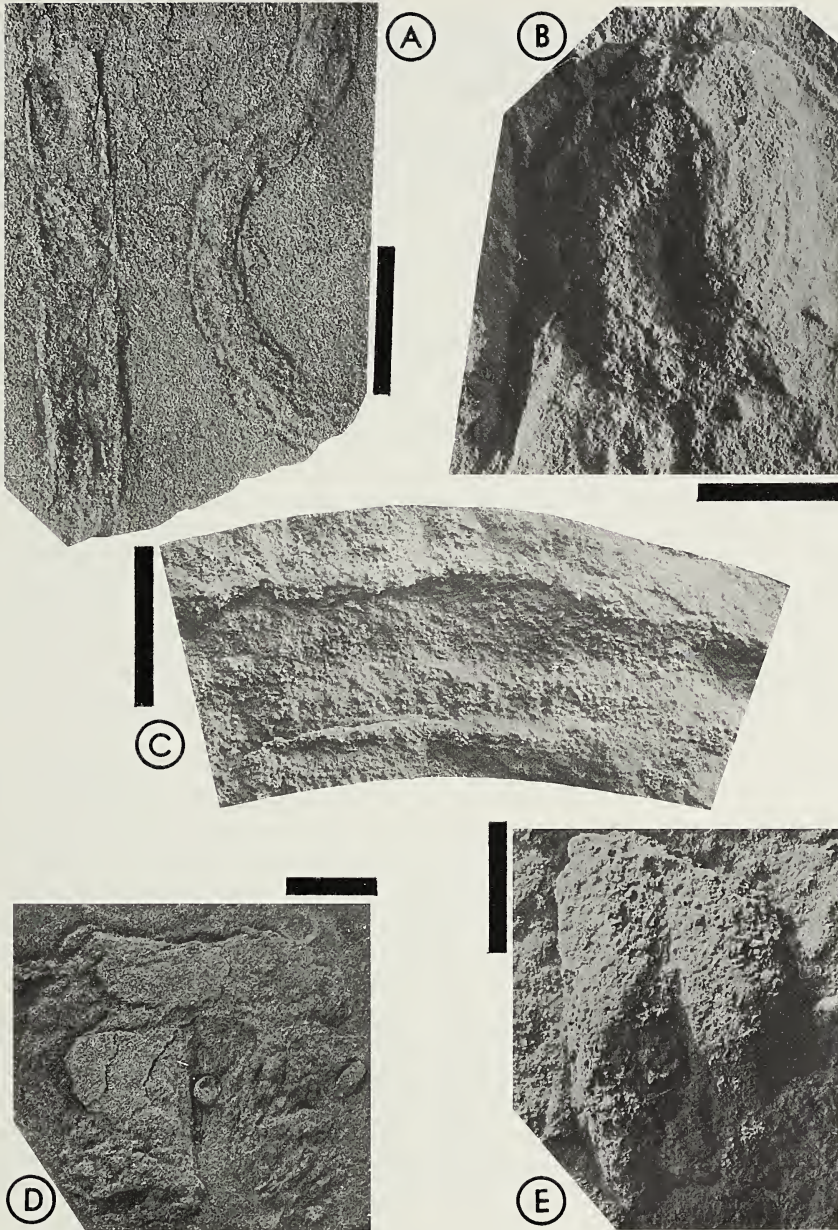


Fig. 11.—A, C. *Psammichnites* ichnospecies. A. KSU 4535, convex epirelief, lithofacies 2, Bridal Veil Falls section. C. KSU 4534, hyporelief counterpart, lithofacies 2, Bridal Veil Falls. B. *Rusophycus* cf. *R. dispar* Linnarsson, note genal and pygidial spine impressions of the trace maker preserved along the left and right posterior margins of the trace; KSU 4674, lithofacies 2, Little Elk Creek section. D. *Rusophycus latus* Webby, KSU 4598, convex hyporelief, lithofacies 3, Little Elk Creek section. E. *Rusophycus* cf. *R. pedroanus* Seilacher, KSU 4671, convex hyporelief, lithofacies 3, Little Elk Creek section. Bar scales represent 1 cm.

cussion under ?*Scolicia* in this section). The Deadwood specimens of *Psammichnites* appear to be morphologically distinct from *Scolicia* due to the lack of parallel sediment strings characteristic of that ichnogenus. The close similarity of the Deadwood *Psammichnites* with the material from the Ratcliffe Brooks Formation warrants assignment to *Psammichnites*; however, given the poor quality of the Deadwood specimens we are reluctant to categorize them as conichnospecific.

Facies.—KSU 4534 was collected 1.5 m above the base of lithofacies 2. KSU 4535 was collected 1 m above the base of lithofacies 2.

Ichnogenus Rusophycus Hall, 1852
Rusophycus cf. *R. dispar* Linnarsson, 1869
(Fig. 11B)

Material Examined.—A single specimen (KSU 4674) collected from the Little Elk Creek section.

Description.—Ovoid, mildly bilobed trace preserved in convex hyporelief; width 24 mm medially, tapering to 19 mm anteriorly and posteriorly; length 30 mm; lobes parallel, separated by shallow medial groove that expands to an oval-shaped gap in the middle of trace. Posteriorly, lobes covered with poorly developed, fine striae less than 1 mm thick, oriented at 40° to midline medially, curving to 25° from midline laterally; grouped six to seven striae per centimeter. Anteriorly, trace differentiated into a triangular-shaped region with indistinct striae. Left lateral margin of trace shows a distinct, 24 mm-long ridge that parallels trace margin; posterior margin shows five spine-like projections; projections widest at trace margin, tapering posteriorly; projections larger at the posterolateral margin, decreasing in size posteromedially. In transverse section, trace 5 mm high; highest part located medially, gradually tapering in lateral and anteroposterior directions.

Discussion.—Tentative designation to *R. dispar* is due to the lack of well-defined scratch marks in the anterior part of the burrow. In well-preserved specimens of *R. dispar*, anterior striae are directed posterolaterally from the midline (Fillion and Pickerill, 1990). Similarities with *R. dispar* from the ?Cambro-Ordovician of Newfoundland include the cubichnion's oval shape, the pronounced medial gap, and the acute angle the posterior striae make with the midline (Fillion and Pickerill, 1990:54, pl. 14, fig. 1). This form is unique in that impressions of the genal and pygidial spines of the presumed trilobite trace maker are preserved. Based on the triangular-shaped anterior margin, the long genal spine impression extending parallel to the lateral margin, and pygidial spine impressions that become larger at the posterolateral margin, the trace may have been constructed by dikelocephalid trilobites, which are similar in gross size and shape to this specimen. Faunal lists given in Kulik (1965) show that dikelocephalids are common at the base of the stratigraphic interval from which this specimen was collected.

Facies.—The specimen was collected 4.5 m above the base of lithofacies 2.

Rusophycus latus Webby, 1983
(Fig. 11D)

Material Examined.—A single specimen (KSU 4598) was collected at the Little Elk Creek locality.

Description.—Quadrangle, bilobed trace preserved in convex hyporelief; width from 36 mm anteriorly to 30 mm posteriorly; length 32 mm; lobes parallel and distinct posteriorly, separated by 4.5 mm-wide median groove. Anteriorly, lobes merge to form a single platform that is approximately one-third the length of trace; platform ornamented with very coarse, transversely oriented striae; anterior striae having a more convergent-divergent pattern than posterior striae. Posterior bilobate section

ornamented with coarse, 0.5–1 mm-thick, parallel striae, oriented at 40° to the midline, numbering eight to 12 striae per lobe; striae finer medially, coarsening laterally. In transverse section: trace shallow, extending no more than 4 mm above bedding; highest part along medioanterior margin, gently tapering laterally and posteriorly.

Discussion.—Seilacher (1970) classified both *Rusophycus*- and *Cruziana*-type traces of presumed trilobite origins under one ichnogenus, *Cruziana*, primarily as a matter of convenience because the two ethological types commonly intergrade. Webby (1982), in an examination of Lower Ordovician trace fossils from New South Wales, found no intergradations between *Cruziana* (furrowing trace) and Seilacher's *C. omanica* (resting type). As a consequence, Webby designated a new ichnospecies, *Rusophycus latus*, as complimentary cubichnia of *C. omanica*. Other reported occurrences of *R. latus* include the Lower Cambrian of California (Alpert, 1976) and Newfoundland (Crimes and Anderson, 1985; Narbonne et al., 1987), ?Cambro–Ordovician formations in Newfoundland (Fillion and Pickerill, 1990), and the Cambro–Ordovician units from Argentina (Mángano et al., in press). Similarities between all these specimens include the overall quadrate shape with a length–width ratio of <1, differentiation in the orientation and thickness of anterior versus posterior striations, lack of grouping of striae into distinct bundles, and the coarseness of the striae.

Facies.—This specimen was collected 8 m above the base of lithofacies 3.

Rusophycus cf. *R. pedroanus* (Seilacher, 1970)
(Fig. 11E)

Material Examined.—Three specimens occur on a single slab (KSU 4671) collected from the Little Elk Creek locality. A single specimen (KSU 4542) was collected at Bridal Veil Falls.

Description.—Longer than wide, bilobed trace preserved in convex hyporelief; width 15 mm, length from 25–30 mm. Individual lobes vary from 7 mm wide anteriorly to 4 mm wide posteriorly; lobes diverge posteriorly, becoming separated by prominent V-shaped median groove that varies from 1–5 mm going from anterior to posterior; surface ornamentation indistinct except for poorly developed, coarse striae on one specimen; striae from 1–2 mm thick; vary from 40–60° to the midline medially, to 70–80° from midline laterally. In transverse section trace shallow, extending 4–6 mm above bedding; lobes steep-sided and broadly semicircular in cross section.

Discussion.—The poor quality of the Deadwood specimens does not allow a definitive assignment to an ichnospecies. Based on the overall shape of the cubichnion, which consists of divergent lobes separated by a distinct V-shaped gap, our specimens resemble *R. pedroanus* from the Upper Silurian of Spain and Libya (Seilacher, 1970:fig. 7.25), and *R. cf. pedroanus* described from the ?Cambro–Ordovician of Newfoundland (Fillion and Pickerill, 1990:56, pl. 15, fig. 5). Other distinguishing characteristics are the very coarse striations on one of our specimens, which was described by Fillion and Pickerill (1990:56) as giving the trace a “corrugated appearance.”

Facies.—KSU 4671 was collected 29 m above the base of lithofacies 3. KSU 4542 was collected 1.5 m above the base of lithofacies 2.

? *Rusophycus* ichnospecies
(Fig. 12C)

Material Examined.—A single specimen (KSU 4669) was collected as float at the Little Elk Creek locality.

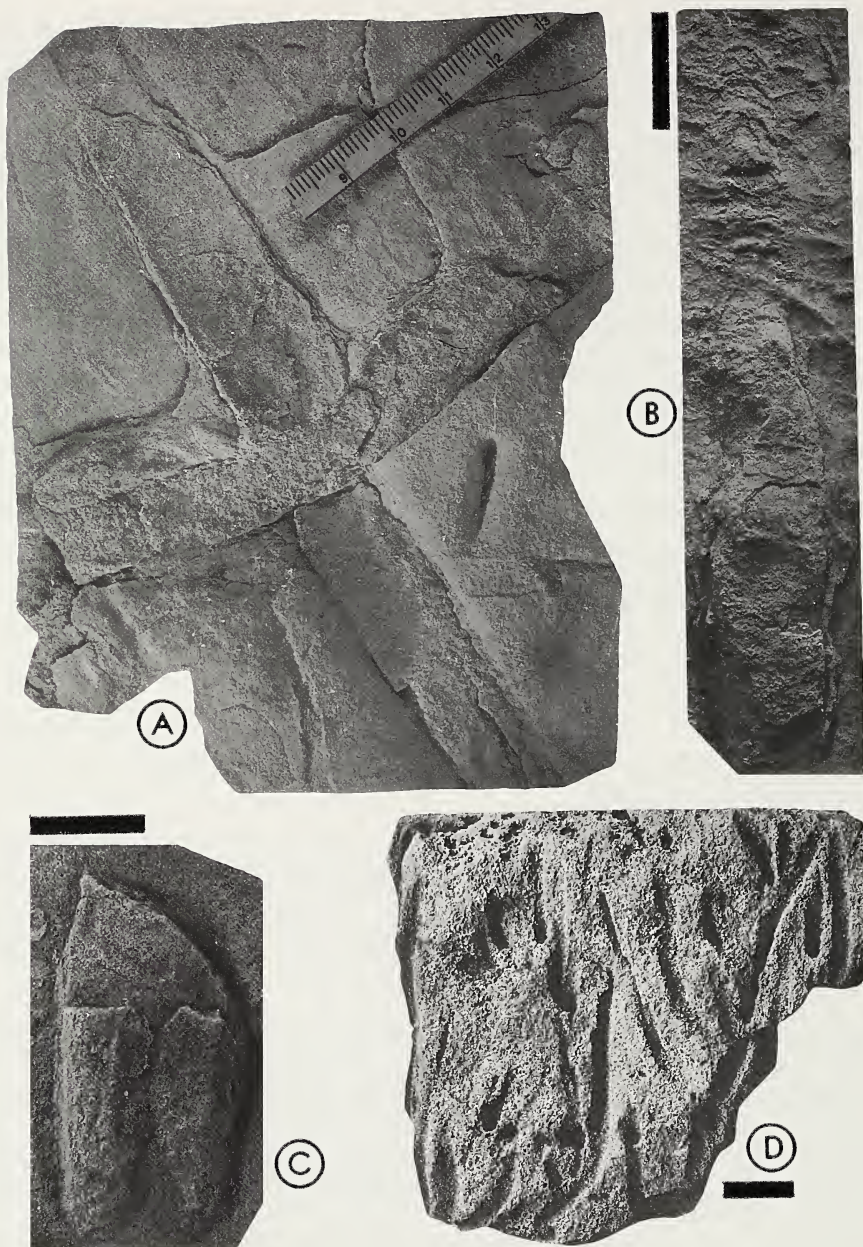


Fig. 12.—A, B. *?Scolicia* ichnospecies. A. KSU 4590, concave epirelief, lithofacies 2, Little Elk Creek section. B. Note arcuate ridges leading to distinct hypichnial ridge; KSU 4681, convex hyporelief, lithofacies 2, Deadwood type section. C. *?Rusophycus* ichnospecies, KSU 4669, convex hyporelief, lithofacies 3, Little Elk Creek section. D. *Skolithos* ichnospecies, typical form found in upper 2 m of the Aladdin Sandstone; KSU 4677, Deadwood type section. Bar scales represent 1 cm.

Description.—Bilobed trace preserved in convex hyporelief; width 17 mm, tapering to 15 mm at posterior(?) end; incomplete length. Lobes parallel, approximately one-half total trace width; separated by shallow medial groove that varies between 2–3 mm wide; groove distinct posteriorly(?), indistinct anteriorly(?). No surface striae evident. In transverse section trace extends 5 mm above bedding; lobes quadrate in cross section, flat crested, and form a steep angle to bedding surface.

Discussion.—Because this specimen is incomplete and poorly preserved, it is uncertain whether it represents a true *Rusophycus* or a broken *Cruziana*.

Facies.—Although collected as float, the slab on which this specimen is preserved is similar to the thin, lenticular siltstone beds described from lithofacies 3.

Ichnogenus *Scolicia* De Quatrefages, 1849

?*Scolicia* ichnospecies

(Fig. 12A, B)

Material Examined.—Two specimens on a single slab (KSU 4590) and another specimen (KSU 4681) were collected from the Little Elk Creek locality. Specimens KSU 4557 and 4572 were collected from the Deadwood type locality.

Description.—Single, large, deep furrow that may become weakly bilobed along its length; preserved in concave epirelief or convex hyporelief; width varies from 10–17 mm, averages 14 mm, remaining constant along trace length within individuals; length variable, maximum measured at 175 mm; furrow floor smooth (KSU 4590; Fig. 12A), composed of a finer-grained material than host matrix that may represent a lining. KSU 4681 (Fig. 12B) represents a single hypichnial ridge that becomes weakly bilobed at terminations; surface of furrow ornamented with fine, arcuate to straight transverse ridges that do not extend to trace margins; ridges grouped five to seven per centimeter. In transverse section epichnial furrow and hypichnial ridge has a quadrate cross section; depth or height of main structure ranges from 5–7 mm.

Discussion.—These specimens were originally assigned to *Palaeobullia* Göttinger and Becker based on similar morphology and mode of preservation with Pennsylvanian forms from Tennessee (Miller and Knox, 1985), and because of similarities with modern gastropod epichnia (Knox and Miller, 1985). Uchman (1995) has subsequently synonymized *Palaeobullia*, *Taphrhelminthopsis*, and *Subphyllochordia* into *Scolicia*. Most of these other forms, particularly *Palaeobullia* and *Taphrhelminthopsis*, represent preservational variates of washed-out *Scolicia*. Two of the Deadwood specimens do have the appearance of postconstruction erosion similar to that illustrated by Uchman (1995:text-fig. 2A, B; Fig. 12A). Uchman (1995) also suggests that similar washed-out traces (*Scolicia strozzii*) are possible preservational variates of *Curvolithus* or *Cruziana*. Neither *Curvolithus* nor *Cruziana* appear to be good candidates for the Deadwood specimens in that they represent a single hypichnial ridge or epichnial groove that is sometimes preceded by arcuate transverse ribs representing backfilling of the burrow (top half of Fig. 12B). The specimen in Figure 12D superficially resembles *Beaconites* illustrated in Häntzschel (1975:pl. 28, fig. 1). *Beaconites*, however, is characterized by a distinct wall enclosing the backfill menisci (D'Alessandro and Bromley, 1987; Keighley and Pickerill, 1994). The Deadwood specimens do not exhibit a wall structure. All specimens from the Deadwood resemble in gross morphology epichnial or hypichnial expressions of washed-out *Scolicia* with poorly developed sediment strings along the bottom of the burrow. The lack of bilobate or trilobate morphology of the Deadwood traces is the reason only tentative assignment to *Scolicia* is made.

Facies.—KSU 4557 and 4572 were collected 3.5 m above the base of lithofacies 2. KSU 4590 and 4681 were collected 4.5 m above the base of lithofacies 2.

Ichnogenus *Skolithos* Haldeman, 1840
Skolithos ichnospecies
(Fig. 7D, 8E, 12D)

Material Examined.—Specimens were collected from all localities and from most lithofacies except for lithofacies 3. Abundant *Skolithos* burrows are the most distinct feature of the upper 2 m of the Aladdin Sandstone.

Description.—Specimens on a large block (KSU 4677; Fig. 12D) are narrow, unbranched, vertical to slightly inclined shafts preserved in full relief; shafts vary between 1–2 mm in diameter, remaining constant in individuals; normally straight, but may curve slightly at distal portions of tube; length variable, maximum observed at 45 mm; walls unornamented. Specimens on slabs KSU 4586 and 4676 (Fig. 7D, 8E) are narrow vertical shafts, having circular to oval cross sections; shafts preserved in convex or concave hyporelief, concave epirelief, or full relief; shaft diameters range from 3–8 mm, average 5 mm, length incomplete; tube usually filled with sediment creating raised pimples in hyporelief and shallow depression in epirelief.

Discussion.—Some of the collected specimens of *Skolithos* from the Aladdin Sandstone (KSU 4677; Fig. 12D) appear conichnospecific to *Skolithos verticalis* (Alpert, 1974). The other specimens of *Skolithos* (KSU 4586 and 4676; Fig. 7D, 8E) are incomplete, but judging by their cross-sectional dimensions, may belong to *S. linearis* (Alpert, 1974). *Skolithos* is common throughout the outer sand-flat lithofacies (lithofacies 2) and off-shore parts of the inner sand-flat lithofacies (lithofacies 1). It is the most diagnostic feature of the upper 2 m of the Aladdin Formation, making the Aladdin one of the most easily recognizable and mappable formations in the Black Hills.

Facies.—Specimens collected and described from the Aladdin Sandstone (KSU 4677) occur within lithofacies 4 and represent a high-energy beach or barrier island complex. Other collected specimens usually occur in groups of ten or more individuals on a single slab and include KSU 4586 and 4676, collected 5 and 6.5 m, respectively, above the base of lithofacies 2 at the type section. At the Little Elk Creek section: KSU 4679 and 4681 were collected 3.3 and 4.5 m, respectively, above the base of lithofacies 2; KSU 4682 was collected 5.3 m above the base of lithofacies 1.

Ichnogenus *Taenidium* Heer, 1877
Taenidium serpentinum Heer, 1877
(Fig. 13A)

Material Examined.—Two specimens occur on a single slab (KSU 4544) collected from the Bridal Veil Falls locality.

Description.—Narrow, unlined, linear trace preserved in convex hyporelief; width 2 mm, maximum length 126 mm; trace margins slightly annulated; trace interior with numerous, regularly spaced, fine, transverse arcuate menisci that represent backfilling of burrow; menisci average 1.6 mm thick in longitudinal direction; grouped 16 menisci per centimeter. In transverse section burrow has semicircular to quadrate cross section; height no more than 2 mm above bedding.

Discussion.—The presence of evenly spaced, gently arcuate menisci that are about as thick as the burrow is wide, and lack of a wall support assignment of these specimens to *Taenidium serpentinum* (D'Alessandro and Bromley, 1987; Keighley and Pickerill, 1994).

Facies.—The specimens were collected 4.8 m above the base of lithofacies 3.



Fig. 13.—A. *Taenidium serpentinum* Heer, KSU 4544, convex hyporelief, lithofacies 3, Bridal Veil Falls section. B, C. *Teichichnus* ichnospecies. B. Full-relief partial burrow intersecting bedding on the left of figure; KSU 4574, lithofacies 2, Deadwood type section. C. Same specimen in transverse profile, note poorly preserved spreite. D. *Thalassinoides* ichnospecies, main burrow labeled as “M,” secondary branches labeled with an “S”; KSU 4589, full relief, lithofacies 3, Little Elk Creek section. Bar scales represent 1 cm.

Ichnogenus *Teichichnus* Seilacher, 1955
? *Teichichnus* ichnospecies
(Fig. 13B, C)

Material Examined.—Specimen KSU 4574 was collected at the Deadwood type section, KSU 4682 from the Little Elk Creek locality.

Description.—Cylindrical burrow oriented parallel to bedding, except at end where it gradually deflects into bedding, preserved in full relief; width 15 mm, remaining constant along burrow length; incomplete length of 55 mm; retrusive spreite arranged as stacked gutters, composed of 0.5–1 mm-thick packages of fine-grained sand and silt, oriented concave-up in cross section and intersect burrow floor at 10–15° in profile; burrow walls ornamented with fine, longitudinally directed striae, formed as exterior expression of the spreite.

Discussion.—There is some possibility of misidentification of incomplete burrows of *Teichichnus*. It has been noted that *Teichichnus* may be transitional to *Rhizocorallium* (Chisholm, 1970), *Ophiomorpha* (Hester and Pryor, 1972; Frey et al., 1978), and *Thalassinoides* (Frey and Seilacher, 1980). None of these other ichnogenera were collected from the Deadwood Formation, except for one possible specimen of ?*Thalassinoides* from the Little Elk Creek section. Because of the incomplete nature of the collected specimens only a tentative assignment is given to the Deadwood forms.

Facies.—KSU 4574 was collected 3.5 m above the base of lithofacies 2. KSU 4682 was collected 8.7 m above the base of lithofacies 1.

Ichnogenus *Thalassinoides* Ehrenberg, 1944
Thalassinoides ichnospecies
(Fig. 13D)

Material Examined.—A single specimen (KSU 4589) was collected from the Little Elk Creek section.

Description.—Cylindrical-shaped burrow system preserved in full relief; burrows oriented horizontal to bedding; incomplete length of main burrow 30 mm; diameter of main burrow 15 mm except at burrow junctions, which swell to 19 mm; secondary burrows slightly smaller than main trunk, diameter 10 mm, oriented at 90° to main burrow; main trunk and secondary bifurcations show regularly spaced constrictions producing an annulated burrow margin; constrictions transverse, slightly arcuate, ranging between 2–5 mm thick in longitudinal direction, grouped two to three annuli per centimeter; internal composition of burrow system different than surrounding matrix. In transverse section burrow cross section oval, with long axis of ellipse parallel to bedding; faint, transverse laminations present, suggesting burrow collapse; bedding of host matrix near burrow system highly disturbed, with top of burrow showing gradational contact with host lithology.

Discussion.—Assignment of this specimen to *Thalassinoides* ichnospecies is based on the branching character and slight swelling of the burrow at branch junctions. Burrow junctions of the Deadwood specimen, however, are at nearly 90°, which is atypical of Late Paleozoic and younger forms assigned to this ichnogenus (Myrow, 1995). However, similar T-shaped, rather than Y-shaped, bifurcations have been reported by Howard and Frey (1984), Bromley (1990:159), Maples and Suttner (1990), Myrow (1995), and Uchman (1995). Until recently, *Thalassinoides* had not been recorded from units older than the Ordovician (Sheehan and Schiefelbein, 1984; Bromley, 1990:159; Myrow, 1995). Myrow (1995), however, has identified a new ichnospecies, *T. horizontalis*, from the Upper Cambrian Peerless Formation of Colorado. There are also possible occurrences of *Thalassinoides* in rocks as old as the Lower Cambrian (Droser and Bottjer, 1988). Similarities between the Deadwood *Thalassinoides* and *T. horizontalis* consist of

a burrow system oriented parallel to bedding with no vertical shafts, burrow junctions are mostly T-shaped and show little to no swelling, lack of definite scratches along burrow walls, and infilling material that is arranged as spreite that is compositionally different from the host matrix. The Deadwood specimen, however, is larger and exhibits slight constrictions along the margins of interjunction segments.

Facies.—This specimen was collected 3 m above the base of lithofacies 3.

Ichnogenus *Trichophycus* Miller and Dyer, 1878

Trichophycus pedum (Seilacher, 1955)

(Fig. 14A)

Material Examined.—Two specimens (KSU 4554, 4578) were collected from the Deadwood type section. A third specimen (KSU 4543) was collected at Bridal Veil Falls.

Description.—Trace preserved in convex hyporelief; consisting of a linear main trunk, ranging from 3–5 mm wide; incomplete length of 65 mm; stout secondary branches arise from midline of main trunk, loop around, and extend upward into host bed; exposed parts of secondary branches not more than 4 mm wide and 6 mm long. Lateral margins of main trunk with faint undulations; margins of secondary branches straight.

Discussion.—Geyer and Uchman (1995:185–187, fig. 5.3–5.5, 6, 7.1–7.9) have recently reassigned this form to *Trichophycus* Miller and Dyer, based on differing behavioral patterns between this ichnospecies and other forms of *Phycodes*. *Trichophycus pedum* consists of a straight to gently winding main burrow oriented horizontal to bedding, with a variable number of secondary lateral probes extending obliquely off the main burrow into the host bed. Geyer and Uchman (1995) note that *T. pedum* exhibits variable morphology that ranges from straight to curved main tunnels, coupled with different densities of the secondary probes. The Deadwood forms show a linear tunnel with sparse secondary probes, which closely resemble *T. pedum* collected from the Lower Cambrian Cándana Quartzite of Spain (Crimes et al., 1977:fig. 7a, b), and a few forms collected from sandstone facies of the Lower Cambrian Gross Aub Formation (Geyer and Uchman, 1995:fig. 7.7). The prime similarity is the straight character of the main tunnel in both the Deadwood and Spanish material compared to the more common, gently curving to palmate morphology represented by material from the Lower Cambrian of Pakistan (Seilacher, 1955), other forms from the Nama Group (Geyer and Uchman, 1995), ?Cambro–Ordovician Kellys Island and Little Bell Island formations (Fillion and Pickerill, 1990), Middle Cambrian Oville Formation of northern Spain (Legg, 1985), Lower Cambrian Breivik Formation of Norway (Banks, 1970), and the Lower Cambrian Random Formation of Newfoundland (Crimes and Anderson, 1985). The straight morphology may be a function of the coarse-grained texture of the hosting sediment, as well as the environment of deposition under which these variates were constructed. The Cándana Quartzite and the hosting lithofacies of the Gross Aub and Deadwood formations are medium- to coarse-grained sandstones in association with desiccation cracks that formed under very shallow, intertidal conditions.

Facies.—Specimen KSU 4554 was collected 2.5 m above the base, and KSU 4578 was collected 5.9 m above the base of lithofacies 1. KSU 4543 was collected at the base of lithofacies 2.

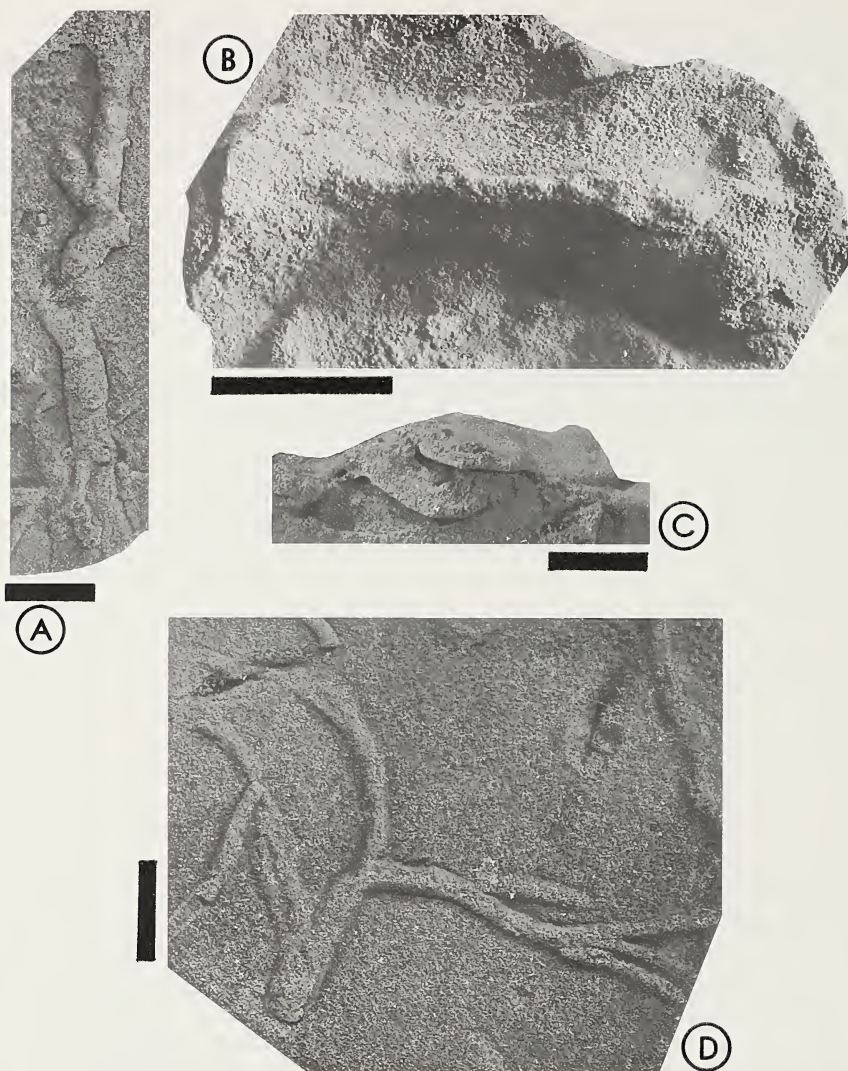


Fig. 14.—A. *Trichophycus pedum* (Seilacher), KSU 4554, convex hyporelief, lithofacies 1, Deadwood type section. B, C. *Uchirites* ichnospecies. B. Full-relief burrow shown from above, note sharp ridge at apex of burrow; KSU 4573, lithofacies 2, Deadwood type section. C. Same specimen seen in cross section, note blunt lower apex of burrow. D. “Branched Burrow,” KSU 4562, convex epirelief, lithofacies 2, Deadwood type section. Bar scales represent 1 cm.

Ichnogenus *Uchirites* Macsotay, 1967

Uchirites ichnospecies

(Fig. 14B, C)

Material Examined.—A single specimen (KSU 4573) collected at the Deadwood type locality.

Description.—Straight tube preserved in full relief; width 10 mm; incomplete length of 15 mm; surface of tube ornamented with faint grooves running parallel to long dimension of trace; trace cross section almond-shaped, with sharp upper apex and blunt lower apex; trace interior hollow, consisting

of a circular tube encased in a sheath-like envelope; envelope composed of a coarser-grained material than host lithology.

Discussion.—A diagnostic character of *Uchirites* is its almond-shaped cross section, consisting of a sharp upper apex and blunt lower apex. The burrow typically consists of an inner structure with a smooth external surface surrounded by an outer structure having the appearance of a sheath (Chamberlain, 1971:231). In well-preserved specimens this outer sheath typically is ornamented by fine striae obliquely oriented to the midline. Although the Deadwood specimen lacks a striated surface, it shows sufficient morphological characters to be classified under *Uchirites*.

Facies.—This specimen was collected 7 m above the base of lithofacies 2.

“Branched Burrow”
(Fig. 14D)

Material Examined.—Specimen KSU 4562 was collected from the Deadwood type section.

Description.—Narrow, unornamented, branched-burrow system preserved in convex epirelief; main burrow 3.5 mm in diameter; second-order branches 2 mm in diameter, typically at 90° to main burrow; third-order burrows typically 1–1.5 mm in diameter; making a 20–25° angle with second-order burrows.

Discussion.—This trace vaguely resembles *Chondrites* Sternberg and *Hartsellea* Rindsberg. Differences between it and *Chondrites* are the higher branch angles and the decrease in burrow diameter in the second- and third-order burrows seen in the Deadwood specimen. *Hartsellea* also represents a branching-burrow system like *Chondrites*, but individual burrows of *Hartsellea* have a distinctly lined wall and internal menisci (Rindsberg, 1994:47–50, pl. 9B, 10A, B, 11A–D, 12C, D). The Deadwood specimen shows no lining or menisci fill.

Facies.—This specimen was collected at the top of lithofacies 2.

“Gently Curved Trace”
(Fig. 15A)

Material Examined.—A single, incomplete specimen (KSU 4533) collected at Bridal Veil Falls.

Description.—Smooth, narrow ridge preserved in convex epirelief. Ridge consistently 1.2 mm wide; circumference is 80 mm, incomplete; ridge gently curves to resemble a half circle.

Discussion.—Because this specimen is incomplete no ichnogeneric designation is given, although it does resemble a partial *Circulichnis montanus* Vialov, 1971 (Häntzschel, 1975:W52, pl. 31, fig. 4; Pickerill and Keppie, 1981:fig. 3). The trace does not appear to have been actively backfilled in that the filling material lacks distinct spreite and menisci, and is of the same composition as the host matrix. This excludes the form as a possible *Planolites* burrow based on taxonomic criteria (Pemberton and Frey, 1982; Keighley and Pickerill, 1995). The trace is also unlined, which would exclude it as a possible *Palaeophycus* (Pemberton and Frey, 1982; Keighley and Pickerill, 1995).

Facies.—Specimen was collected 1.8 m above the base of lithofacies 3.

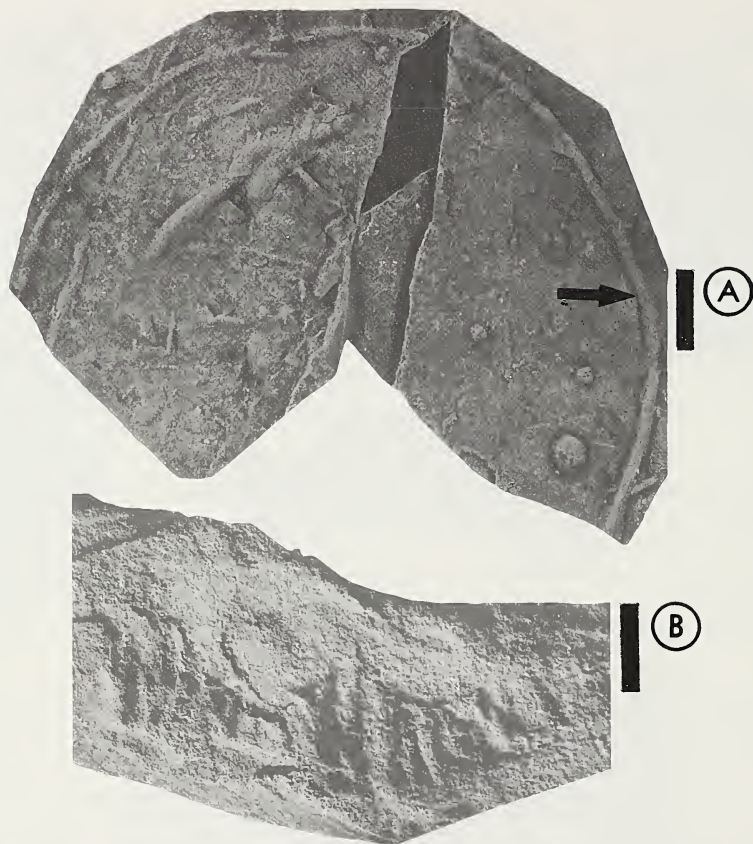


Fig. 15.—A. “Gently Curved Trace” shown by arrow, KSU 4533, lithofacies 3, Bridal Veil Falls section. B. “Ribbed Trail,” KSU 4573, concave epirelief, lithofacies 2, Deadwood type section. Bar scales represent 1 cm.

“Ribbed Trail”
(Fig. 15B)

Material Examined.—A single specimen (KSU 4573) collected at the Deadwood type section.

Description.—Slightly curving furrow preserved in concave epirelief; furrow width approximately 20 mm; incomplete length 50 mm; furrow with regularly spaced transverse ridges; ridges consistently 2 mm thick in longitudinal direction, spaced 3 mm apart, and do not extend to lateral margins of furrow.

Discussion.—The poor preservation of the specimen does not support a formal ichnogenic designation. However, the trace looks very similar to the epichnial groove part of *Plagiogmus* Roedel (Glaessner, 1969:385, fig. 8).

Facies.—Specimen was collected 7 m above the base of lithofacies 2.

RESULTS

Aspects of Cambro-Ordovician Sedimentation

Sedimentary structures consisting of bidirectional crossbedding, clay drapes, flaser, wavy, and current-rippled bedding, and the occurrence of mudcracks in

siltstone and sandstone beds indicate that lithofacies 1 and 2 were deposited under intertidal conditions (Ginsburg, 1975:92; Klein, 1985). The fine-grained terrigenous clastics intermixed with tempestite-derived intraclastic limestones in lithofacies 3 indicate that this unit was deposited further offshore on the Cambro-Ordovician shelf. The chaotic nature of the intraclasts suggests little postdepositional reworking by tidal currents or waves, implying deposition below normal wave base, but not below storm wave base. The lenticular nature and curved lower contacts of the intraclastic beds suggest scouring of the substratum during tempestite deposition. A similar interpretation was made for Deadwood time-equivalent units in Montana (Emerson Formation) and Wyoming (Du Noir Formation; Sepkoski, 1982), which also consist of interbedded shale and intraclastic limestone.

Other published examples of Cambro-Ordovician siliciclastic tidal deposits include the Eureka Quartzite of California and Nevada (Klein, 1975), the Monkman Quartzite of western Canada (Jansa, 1975), the Hickory Sandstone of central Texas (Cornish, 1986), the Theresa-March formations of New York and Ontario (Bjerstedt and Erickson, 1989), the upper Bell Island and Wabana groups of Newfoundland (Fillion and Pickerill, 1990), and the Santa Rosita Formation of Argentina (Mángano et al., in press). Except for the Bell Island and Wabana groups, all of these formations conform lithologically and texturally to the Deadwood-Aladdin tidal deposits. Similarity among these regionally separated deposits is illustrated by the lack of terrigenous mud in the upper intertidal to supratidal regimes. In contrast, Late Paleozoic (Carboniferous) to Recent tidal environments contain a predominance of mud in upper tidal facies (Ginsburg, 1975; Weimer et al., 1982; Klein, 1985); because tidal-flat facies models have been based on these Recent mud-dominated tidal sequences, recognition of Lower Paleozoic tidal deposits have been difficult (Dott and Byers, 1980; Klein, 1980; Moiola, 1980). For example, units previously interpreted as simple blanket sands that formed under wave-dominated coastal systems such as the Middle Cambrian Flathead Sandstone of Wyoming and Montana, the Lower Ordovician St. Peter Sandstone of the mid-continent, and the Mt. Simon and Eau Claire formations of Wisconsin exhibit a greater complexity and intergradation of tidal and nonmarine fluvial sedimentation than previously reported (Dott and Byers, 1980; Moiola, 1980; Driese et al., 1981; Bjerstedt and Erickson, 1989).

Lack of a dominant mud facies in these Cambro-Ordovician tidal orthoquartzite suites may be due to the extreme macrotidal range of the Cambrian epeiric seas, coupled with an absence of vascular plants. Given the low-lying topography of the Precambrian basement during the initial Cambrian transgressions onto the craton, frictional drag would have minimized wave processes while augmenting tidal ranges and currents in nearshore coastal settings (Irwin, 1965; Schopf, 1980; Hallam, 1981; see Fig. 2). Assuming horizontal time lines in Figure 4, a minimal breadth of the Black Hills Cambro-Ordovician shelf intertidal zone may have approximated 25–35 km, which far exceeds the 7-km average of modern macrotidal coasts (Klein, 1980; Weimer et al., 1982). The closest modern analog that can be compared to the Deadwood-Aladdin intertidal zone is the Yellow Sea macrotidal flat of southwestern South Korea, with a tidal-flat width ranging from 8–25 km (Klein, 1980; Alexander et al., 1991). Current energy produced by tidal forces was probably fairly strong, especially across shelf areas within effective wave base. Lithofacies 2 is interpreted as forming in a moderate- to high-energy tidal regime due to the occurrence of parting lineations on some siltstone and

sandstone bedding surfaces, and probably falls within the high-energy region of Irwin's model for epicontinental seas (Irwin, 1965; Hallam, 1981; see Fig. 2). Current energy probably slackened over the inner parts of the tidal flats, exemplified by lack of well-developed bedforms and tidal sedimentary structures in lithofacies 1, compared to lithofacies 2. Lack of fine-grained terrigenous clastics in lithofacies 1 suggests that tidal energy was strong enough to wash all but a coarser-grained sand fraction basinward. Transportation of muds basinward was also permitted by the lack of baffling by vascular plants in the upper intertidal and supratidal zones during the Early Paleozoic. Tidal deposits in Texas and New York also exhibit a coarsening of grain size in the upper peritidal to supratidal parts of the sand flats (Cornish, 1986; Bjerstedt and Erickson, 1989). Except for thin shale partings and clay drapes in lithofacies 2, the mud fraction by-passed the intertidal zones, and was deposited further offshore in lithofacies 3 (Fig. 16).

Besides their trapping effects of fine-grained siliciclastics in upper tidal areas, the importance of vascular plants today can be inferred by changes in the type of physical and chemical weathering in terrestrial environments throughout geologic time. Without terrestrial plants, eolian processes probably dominated land areas in the Early Paleozoic, and without the stabilization effects of plants, would have deposited a greater amount of coarse-grained sand in nearshore marine environments than observed today (Dott and Byers, 1980). At least for terrigenous tidal deposits, tidal sedimentation has changed since the Cambrian, and may be directly or indirectly related to the exploitation of the inner tidal zone by vascular plants, and strong tidal currents prevalent along ancient mesotidal coasts.

The nature and trophic structure of tidal-flat benthic communities also must have changed with the evolution of vascular plants because of the indirect effect on substrate type within Cambro-Ordovician upper intertidal regimes. Modern macrotidal flats such as the Yellow Sea coast of South Korea and Gulf of California are characterized by large numbers of epifaunal, herbivorous grazers and deposit feeders in the inner tidal environments (Thompson, 1968, 1975; Frey et al., 1987; Fürsich and Flessa, 1987). Herbivorous gastropods and bivalves dominate these modern peritidal and supratidal environments, feeding on algae and plant detritus deposited from suspension from waning tidal currents (Fürsich and Flessa, 1987). Consequently, there is a preponderance of epifaunal repichnia- and infaunal vertical domichnia-type traces in Recent upper tidal regimes (Frey et al., 1987). Traces common to the upper tidal zones of the Deadwood Formation differ considerably from the modern counterparts (Table 1). Horizontal infaunal burrows are the most common traces found. These assemblages are dominated by *Planolites*, with minor occurrences of *Palaeophycus*, *Trichophycus*, and ?*Teichichnus*. Although vertical domichnia burrows are present in the upper tidal flats, they are subordinate to the horizontal burrows. Also contrary to Recent tidal assemblages, repichnial surface trails are noticeably sparse in the upper sand flats of the Deadwood (lithofacies 1). However, repichnia do increase in diversity and density in the outer sand-flat deposits (lithofacies 2). A similar situation occurs in the Cambro-Ordovician Marsh-Theresa tidal deposits as the epifaunal-infaunal ratio increases from peritidal to lower intertidal deposits (Bjerstedt and Erickson, 1989) and in the Ordovician Santa Rosita Formation of Argentina, which is characterized by a monochnospecific *Planolites montanus* trace-fossil assemblage in the most shoreward tidal facies (Mángano et al., in press).

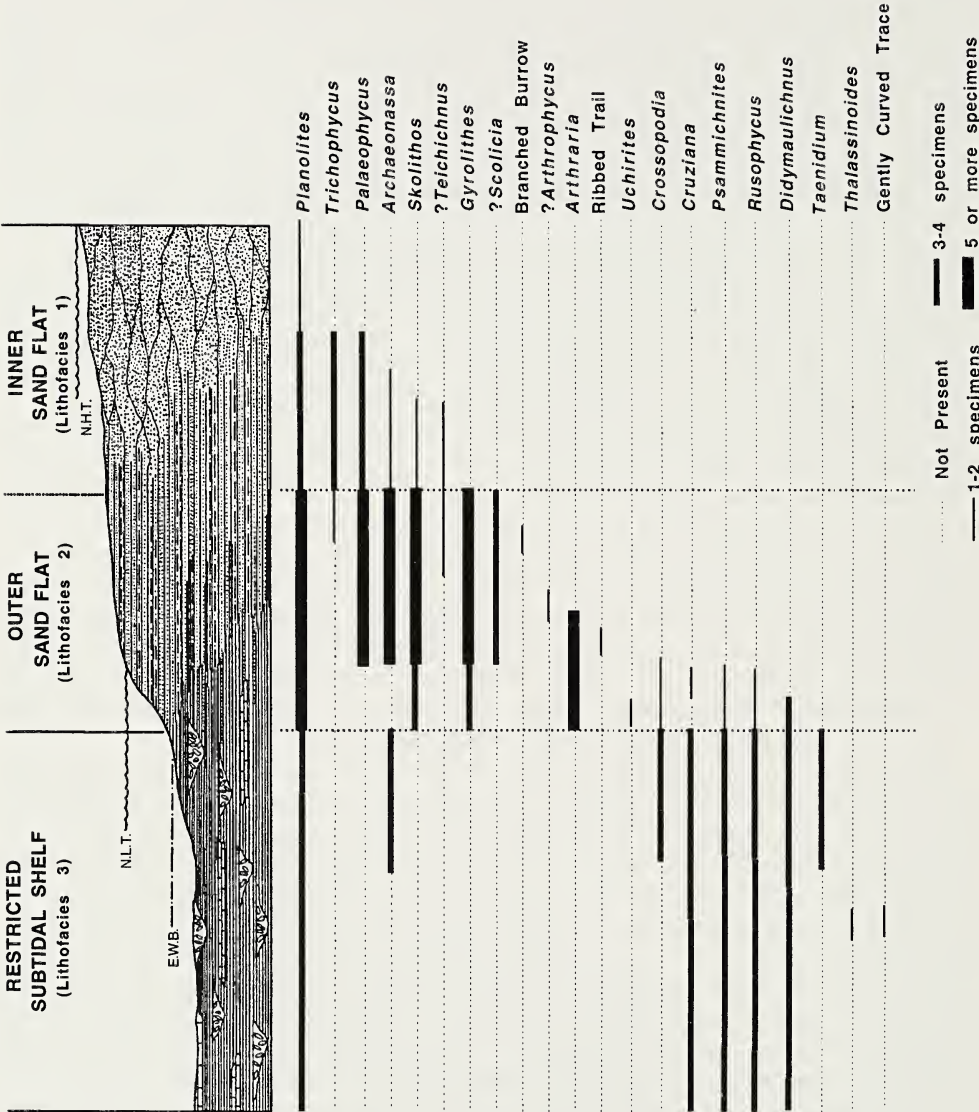
Trace-fossil Assemblages

When coupled with the Deadwood and Aladdin lithofacies, the trace-fossil assemblages provide a clearer picture of Cambro–Ordovician nearshore paleoenvironments. The Deadwood–Aladdin trace fossils can be segregated into distinct assemblages related to the hydrodynamic and sedimentological conditions that persisted during the Cambro–Ordovician of the Black Hills. These assemblages also recur within their prescribed lithofacies during repeated shifting of strand lines (Fig. 4, 16). Two basic trace-fossil assemblages dominate: 1) an intertidal sand-flat assemblage that occurs in lithofacies 1 and 2, and 2) a restricted subtidal-shelf assemblage corresponding to lithofacies 3. Trace fossils also reflect sedimentologic and taphonomic regimes within the intertidal environment, and can be segregated into an inner sand-flat assemblage (traces enclosed in lithofacies 1) and an outer sand-flat assemblage (traces enclosed in lithofacies 2). Table 1 summarizes the trace fossil distribution with corresponding lithofacies types.

Inner Sand-flat Assemblage.—This assemblage is characterized by very low ichnofaunal density and diversity, and occurs in lithofacies 1 and shoreward parts of lithofacies 2 (Table 1; Fig. 16). Ichnotaxa are dominated by *Planolites*. *Palaeophycus*, *Skolithos*, *Trichophycus*, and ?*Teichichnus* also occur, but are rare and normally found in the offshore parts of the assemblage (Fig. 3, 16).

The paucity of trace fossils observed in these inner sand flats contrasts with modern tidal flats, which normally show low diversity but high density of traces within the inner-tidal regimes (Weimer et al., 1982; Ekdale et al., 1984:177; Frey et al., 1987). Environmental parameters such as salinity, temperature, current energy, and subaerial exposure probably varied greatly within these inner-tidal regimes as they do in modern environments, and probably influenced the number and distribution of the trace fossils. Also important are the potential taphonomic effects inherent in very nearshore marine settings (Bromley, 1990) in that the ichnological distinction between the inner and outer sand-flat assemblages may be as dependent on taphonomy, particularly depth of burrowing, as it is on the varying environmental conditions across the intertidal zone.

Although there are noted exceptions in the depth and degree of bioturbation for Lower Paleozoic rocks (Miller and Byers, 1984; Sheehan and Schiefelbein, 1984), burrowing depths of the Cambro–Ordovician marine benthos were shallow (Ausich and Bottjer, 1982, 1990, 1991; Thayer, 1983; Bottjer and Ausich, 1986) and confined to the uppermost mixed-layer tiers (Bromley, 1990:128; Bromley and Asgaard, 1991). Shallow trace construction is also common in modern intertidal environments (Frey et al., 1987). Added to the preponderance of shallow traces, Frey et al. (1987) noted that few of these epibenthic traces in the shoreward parts of the Yellow Sea tidal flats would have little potential for being preserved. It stands to reason that most biogenic activity in the Deadwood inner sand-flat regime stood a fairly poor chance of being preserved as well. The prevalence of disrupted bedding associated with the Deadwood inner sand-flat trace-fossil assemblages may indicate that intense bioturbation occurred without subsequent preservation of discrete, recognizable trace fossils. When comparing the type and distribution of ichnotaxa between the inner and outer sand-flat assemblages, ichnofaunal differences are not as much a change in ichnotaxa, but an exclusion of inferred, shallowly constructed biogenic structures. Full-relief burrows of *Planolites*, *Palaeophycus*, and *Skolithos* are the most common traces in the inner sand-



flat assemblage. It is only toward the more offshore parts of the assemblage that shallower trace fossils such as *Archaeonassa* are preserved (Table 1; Fig. 3, 16).

Substrate type also would have been a factor in trace-fossil preservation, particularly the grain size of the hosting medium. The fact that the lithofacies associated with this assemblage is coarser grained and monotextured compared to the outer sand-flat lithofacies would have contributed to the subtle ichnological and taphonomic differentiation of the intertidal assemblages. The coarse texture of the sediment common to the inner sand flats may have led to the exclusion of other ichnospecies of *Palaeophycus* (besides *P. tubularis*) where taxonomic criteria are based on the delicate ornamentation of the burrow lining, which may not have been preserved in the coarser sediment.

Environmental parameters like current energy, oxygenation, and salinity also played an important role in defining the character of the inner sand-flat assemblage. What is apparent in Figures 3 and 16 is the presence of complex fodinichnia like ?*Teichichnus* and *Trichophycus*, and epichnia like *Archaeonassa* in the more offshore, and assumed more normal, marine parts of the assemblage. Absence of these trace fossils in shoreward parts of the assemblage is probably due to an environmental gradient occurring perpendicular to depositional strike.

Ecological stress acting across the inner-flat benthos is also implied by the average size of the preserved ichnotaxa compared to those same ichnotaxa in the outer flat. Modern outer- and inner-flat areas, such as in the Gulf of California, exhibit a shoreward decrease in size of organisms, particularly mollusks, inhabiting both tidal regimes (Fürsich and Flessa, 1987). Inner-flat gastropods and bivalves were considerably smaller, even within the same species, than their outer-flat counterparts (Fürsich and Flessa, 1987). The authors did not have a definitive explanation for this phenomenon, but stated it could be attributed to either the ecological factors inherent of the stressful inner-flat environments, or to waning current energy across this nearshore area that transported only the smaller species from the outer flat. Within the Deadwood Formation, *Planolites* occurred with high frequency in all lithofacies, represented by *P. montanus* and *P. beverleyensis*. Ichnospecific distinction of these two forms is based primarily on the size of the specimens. *Planolites beverleyensis* has trace diameters 5–8 mm larger than *P. montanus* (Pemberton and Frey, 1982). In all measured sections, *P. montanus* was the only *Planolites* ichnospecies collected from lithofacies 1, suggesting that larger forms of the *Planolites*-producing animal were excluded from inner sand-flat environments. A similar situation occurs in the Lower Ordovician Santa Rosita Formation in Argentina, where high intertidal lithofacies consist of monoichnospecific trace-fossil assemblages of *P. montanus* (Mángano et al., in press). Trace-fossil assemblages in the offshore parts of the intertidal zone of the Santa Rosita show a greater degree of trace-fossil complexity and diversity compared to the *P. montanus* assemblage. This contrast between inner and outer tidal-flat trace-fossil assemblages appears similar to the transition between lithofacies 1 and lithofacies 2 of the Deadwood Formation, and indicates similarities between many Cambro–Ordovician intertidal deposits. Size trends are also observed in burrows of *Pa-*

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Fig. 16.—Lateral distribution of collected ichnogenera and environments of deposition during time T of Figure 4. No vertical or lateral scale is implied. N.H.T. and N.L.T. represent normal high tide and normal low tide, respectively. E.W.B. represents effective wave base.

laeophycus tubularis, which are 7 mm smaller in diameter in lithofacies 1 as compared to lithofacies 2 (see discussion under *Palaeophycus tubularis* in Systematic Ichnology). Differences in the size of trace fossils also were noted by Hakes (1985) from Upper Pennsylvanian marginal-marine settings of Kansas. Hakes (1985:31, table 2) showed that many of the trace fossils from nearshore brackish-water facies were much smaller than those same trace fossils from normal marine facies. This decrease in size was attributed to variable salinities encountered in the marginal-marine trace-fossil assemblages, which probably inhibited the trace makers from attaining full adult size.

It seems unlikely that selective destruction of larger burrows contributed to the size differences between the outer sand-flat and inner sand-flat trace fossils. The analogy can then be drawn between the Deadwood intertidal assemblages and those exhibited by bivalves and gastropods from the Gulf of California, suggesting that size variability in taxa across the intertidal zone is due to ecological factors.

Outer Sand-flat Assemblage.—Ichnotaxa diagnostic of this assemblage includes *Archaeonassa*, *Skolithos*, *Gyrolithes*, ?*Scolicia*, *Arthraria*, and *Planolites beverleyensis* (Table 1; Fig. 16). This assemblage is characterized by an increase in numbers and diversity of ichnogenera compared to the inner sand-flat assemblage. Endobenthic domichnia and fodinichnia of *Palaeophycus*, *Skolithos*, *Planolites*, and *Trichophycus*, and repichnion of *Archaeonassa* increase markedly. New ichnotaxa represented by domichnia (*Arthraria*) and fodinichnia (*Psammichnites*, *Gyrolithes*, and ?*Scolicia*) are also encountered, and indicate more epibenthic and shallow endobenthic modes of life. Trilobite cubichnion and repichnion in the form of *Rusophycus* and *Cruziana* also occur, but are relegated to the more offshore parts of the assemblage. Stronger current action and more normal-marine open circulation, implied by the presence of planar laminations and current-rippled bedding surfaces, accompanies the increased ichnogenetic diversity. The combination of normal-marine circulation and tidal-dominated primary sedimentary structures suggest that this trace-fossil assemblage inhabited an offshore, moderate- to high-energy part of the tidal flat.

Preservational acuity of the different ethological trace fossils increases in the outer sand-flat assemblage, and is directly related to increased sediment heterogeneity found in lithofacies 2. Important to the preservation of surface and near-surface biogenic structures would have been clay drapes deposited from waning tidal currents. These clay drapes, represented as thin shale partings and flaser bedding, would have protected the epichnial and shallow endichnia from erosion at times of exposure and resubmergence of the assemblage during the transition from low to high tide. Conversely, lack of an appreciable mud or fine-grained sand component in the inner sand-flat environment probably contributed to the poor preservational quality of that assemblage.

A strong ecological gradient still occurred across the outer sand flats as *Rusophycus* and *Cruziana* only occur in the offshore parts of the assemblage (Fig. 3, 16). Lack of these ichnogenera in the more landward parts of the outer sand flat suggests that environmental conditions were still too hostile for normal-marine trilobites. Other ichnogenera that overlap from the lower energy areas of the subtidal zone include *Crossopodia* and *Didymaulichnus* (Fig. 16), and imply that environmental conditions were more hospitable for their trace makers toward the offshore parts of the sand flats.

Both the outer and inner sand-flat assemblages represent a mixed or overlapping *Skolithos*–*Cruziana* ichnofacies. Displacement or total absence of a particular ich-

nofacies from the archetypical ichnofacies model has been well documented (Ekdale, 1988; Bromley, 1990; Frey et al., 1990). A notable example for a modern tidal flat is from the Yellow Sea, which falls entirely within the *Cruziana* ichnofacies, with no *Skolithos* ichnofacies shoreward (Frey et al., 1987). A mixed ichnofacies is commonly found in modern and ancient environments that exhibit fluctuating depositional and taphonomic conditions, such as intertidal and estuarine environments (Ekdale et al., 1984:172, 179; Ekdale, 1985; Bjerstedt, 1988). Within the outer sand-flat assemblage current energy was probably the most variable environmental parameter. Strong currents suggestive of bed-load transportation are implied by the presence of parting lineations, cross-bedding, and current-rippled bedding surfaces, while the presence of shale partings and flaser bedding implies suspended-load deposition from waning tidal currents. The net result is a mixed trace-fossil assemblage and taphonomic signature characterizing both high and low current energy.

Restricted Subtidal-shelf Assemblage.—This trace-fossil assemblage corresponds to lithofacies 3 (Fig. 3, 16). Cubichnia and repichnia (*Rusophycus* and *Cruziana*) dominate and are the most diagnostic ichnotaxa of this assemblage. Other ichnotaxa include repichnia of *Archaeonassa* and *Didymaulichnus*, and fodinichnia of *Taenidium*, *?Arthropycus*, *Planolites*, *Psammichnites*, *Crossopodia*, and *Thalassinoides* (Table 1; Fig. 16). The presence of fine-grained terrigenous and carbonate sediments, well-developed, thin to fissile bedding, coupled with epibenthic cubichnia and repichnia suggests that this facies formed in a subtidal, normal-marine environment characteristic of the *Cruziana* ichnofacies. Siliciclastic deposition was sporadic, allowing deposition of carbonate sediment during times of low siliciclastic influx. Periodic storms eroded carbonate sediment from peritidal banks to the west (Fig. 2) and redeposited the flotsam as lenses of intraclastic limestones. Little or no wave reworking is evident in the intraclasts, indicating that this lithofacies formed below normal wave base but not below storm wave base.

Previous paleoecological studies interpreted this lithofacies as forming on intertidal mud flats (Lochman-Balk, 1964, 1970, 1971; Lochman-Balk and Wilson, 1967). However, the taphonomy of the preserved trace fossils, characterized by finely preserved epibenthic and shallow endobenthic traces, coupled with the chaotic nature of the intraclastic limestones, contradicts an intertidal interpretation of this lithofacies. The high diversity but low abundance of traces characteristic of this assemblage suggests periodic disruption of the normal-marine benthos. Low abundance of trace fossils is an ecological response of the benthic community to storm surges that inhibited the establishment of well-developed communities in the substrate. A similar association was noted by Pemberton and Frey (1984) and Vossler and Pemberton (1988) for mixed quiet-water and tempestite deposystems in the Upper Cretaceous of Alberta.

One apparent irregularity of this assemblage is the low density of endobenthic fodinichnia compared to the outer sand-flat assemblage. The lack of strong bioturbation is documented by the well-developed fissility of the shales and absence of burrow mottling in the micritic limestones. The absence of large numbers of infaunal traces may also have been a response to tempestite deposition, but it seems more likely due to hardground or firmground development, which tends to decrease endobenthic activity and trace fossil diversity (Ekdale, 1988). Hardground to firmground development on intraclastic limestones and on some micritic limestone beds is suggested by the presence of expansion cracks on limestone bedding

surfaces formed during early cementation, as well as by protrusion of intraclasts above bedding. The environmental interpretation of subtidal deposition coupled with early cementation in this lithofacies is also supported by Myrow (1995), who noted a strong correlation between the ichnogenera *Thalassinoides* and firmground to hardground development. *Thalassinoides* also appears to be restricted to intertidal and shallow subtidal environments of deposition. Although *Thalassinoides* is not common in this assemblage, its presence strengthens the interpretation that hardground development may have played a part in restricting bioturbation and trace-fossil density. Hardground development is not unique to this lithofacies, and has been documented from similar units in Montana and Wyoming (Brett et al., 1983).

CONCLUSIONS

Combining lithostratigraphic and ichnologic data is an extremely effective aid in deciphering Deadwood-Aladdin paleoenvironments. Sedimentological and hydrodynamic responses of the enclosed ichnotaxa allowed for segregation of intertidal deposystems into two assemblage zones, an inner and outer tidal flat. Due to the extreme changes in environmental and taphonomic parameters, the trace-fossil assemblage enclosed in the inner-flat environment is characterized by low ichnofaunal diversity and abundance. Parameters such as salinity, water temperature, current energy, and sediment heterogeneity greatly influenced the character of this assemblage. Key ichnotaxa that differentiate the outer sand flat from the inner sand flat include: *Archaeonassa*, *Skolithos*, ?*Scolicia*, *Gyrolithes*, *Arthraria*, and *Planolites beverleyensis*. Taphonomic characteristics, as well as changes in the size of the preserved trace fossils, can also be used as guides in segregating the intertidal assemblages.

The subtidal shelf assemblage is characterized by an increased number of shallow repichnia and cubichnia compared to the intertidal assemblages. Main environmental controlling factors on this assemblage appear to be frequent tempestite deposition that may have temporarily disrupted the quiet-water benthos. Lack of deep burrowing ichnofauna within this assemblage may also have been due to the periodic storms that would have exposed firmground or hardground surfaces, and inhibit deep infaunal burrowing.

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DIADECTES (DIADECTOMORPHA: DIADECTIDAE) FROM THE
EARLY PERMIAN OF CENTRAL GERMANY, WITH
DESCRIPTION OF A NEW SPECIES

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ABSTRACT

A new species of the diadectomorph *Diadectes*, *D. absitus*, is described on the basis of a nearly complete, articulated skeleton that includes the skull, an isolated skull, and the greater portions of two articulated postcrania. All were collected from fluvial red-bed deposits immediately above the Tambach Sandstone, middle part of the Lower Permian Tambach Formation, lowermost formational unit of the Upper Rotliegend, of the Bromacker locality in the midregion of the Thuringian Forest near Gotha, central Germany. *Diadectes absitus* represents the first member of this genus to be described from outside of North America. A combination of autapomorphic and plesiomorphic characters provides a more substantial basis for recognizing *D. absitus* than is available for distinguishing between the North American species of *Diadectes*. Two possible conclusions are drawn from the relationship of *D. absitus* to the North American members of the genus: 1) its uniqueness reflects the wide geographic separation from the North American species, and 2) its greater primitiveness reinforces previous assessments of the biostratigraphic position and age of the Tambach Formation as earliest Permian Wolfcampian.

KEY WORDS: Diadectidae (*Diadectes*), Upper Rotliegend, skeleton, Bromacker locality, Germany, Pangaea

INTRODUCTION

Until very recently, the presence of diadectids in the Lower Permian of Europe has been limited to two very incomplete specimens described over a century ago from the Lower Rotliegend of Germany. A string of four presacrals and two sacrals from the Leukersdorf Formation of the Erzgebirge Basin near Zwickau was described by Meyer (1860) as *Phanerosaurus naumanni*, and Geinitz and Deichmueller (1882) described *P. pugnax* on the basis of disarticulated skull and postcranial elements from the Niederhaeslich in the Doehlen Basin near Dresden. In a lengthy restudy of the latter species, Stappenbeck (1905) reassigned it to a new genus as *Stephanospondylus pugnax*. Although the dentition and/or vertebrae of both forms clearly justifies a diadectid assignment, the lack of additional discoveries has not permitted detailed comparisons with the better known diadectids, particularly *Diadectes* of North America, and both of the German taxa remain poorly defined (Romer, 1925).

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During a period of nearly two decades, four specimens assignable to *Diadectes* as a new species have been recovered from a sandstone quarry known as the Bromacker locality that lies in the Lower Permian Tambach Formation, lowermost unit of the Upper Rotliegend, in the middle part of the Thuringian Forest near Gotha, central Germany (Berman and Martens, 1993; Sumida et al., 1996). The first specimen discovered, consisting of a nearly entire, slightly disarticulated postcranial skeleton, was collected by Martens and Schneider in 1979 during an exploratory excavation at the Bromacker quarry, but was misidentified as possibly a limnoscelid diadectomorph (Martens, 1980, 1988, 1989; Martens et al., 1981). In the summer of 1991, Martens discovered a nearly complete, isolated small skull of a juvenile specimen which he identified as a diadectid in a brief note (Martens, 1992). Two closely associated adult specimens were collected by the authors in the summer of 1993. One consists of a nearly complete, articulated skeleton with an excellently preserved skull (designated here as the holotype of a new species) and the other the greater portion of an articulated postcranium. Collectively, these specimens represent the first occurrence of *Diadectes* outside of the Lower Permian of North America.

The Bromacker *Diadectes* is part of a diverse assemblage of terrestrial or semiterrestrial amphibians and reptiles represented by articulated skeletons from the Bromacker locality (Martens, 1980, 1988, 1989; Boy and Martens, 1991; Berman and Martens, 1993; Sumida et al., 1994, 1996). To date, three Bromacker vertebrates have been described: 1) a single, nearly complete skeleton of a new genus of protorothyridid amniote, *Thuringothyris mahlendorffae* Boy and Martens, 1991; 2) two specimens of the seymouriamorph amphibian *Seymouria* were tentatively referred to *S. sanjuanensis* Vaughn, 1966 (Berman and Martens, 1993); and 3) a skull and partial, articulated postcranium representing a new genus and species of the amphibian family Trematopidae (Sumida et al., 1994). *Seymouria* and trematopids are known otherwise only from the Early Permian and Permo-Pennsylvanian, respectively, of North America.

For over a century the Bromacker locality has been well known as a very important source of excellently preserved tetrapod trackways preserved in the Tambach Sandstone of the Tambach Formation (Pabst, 1896, 1908; Müller, 1954, 1969; Haubold 1971, 1973). Vertebrate skeletal remains, however, eluded detection at Bromacker until 1974 (Martens, 1980). All of the vertebrate skeletal specimens so far collected from Bromacker have come from fluvial red-bed facies immediately above the sandstones yielding the trackways and are quite similar to those deposits which have yielded the vast majority of the Lower Permian and Permo-Pennsylvanian vertebrates of the United States (Martens, 1975, 1982, 1988, 1989; Martens et al., 1981; Berman and Martens, 1993; Sumida et al., 1996). With the exception of Bromacker, terrestrial or semiterrestrial vertebrates from Permian red-bed deposits of the Rotliegend or their equivalent in central and western Europe are quite rare and include most notably the primitive synapsids, *Haptodus* (Paton, 1974; Currie, 1979; Laurin, 1994), *Ophiacodon* (Paton, 1974), and *Sphenacodon* (Paton, 1974) from England and *Casea* (Sigogneau-Russell and Russell, 1974) from France.

The apparent uniqueness of Bromacker among European localities has been explained as possibly an artifact of collecting (Martens, 1989; Berman and Martens, 1993; Sumida et al., 1996). The red-bed exposures of the Upper Rotliegend are very poor and have been commonly perceived as representing an inhospitable dry climate that was not conducive to preservation of skeletal remains. As a result,

relatively little energy has been devoted to their exploration, and, as a consequence, they have yielded few vertebrates. Alternatively, intensive prospecting has focused on the highly fossiliferous lacustrine grey sediments and black shales of the Lower Rotliegend that reflect limnetic environments. These deposits, in which are found the well-known tetrapod localities as Niederhaeslich, Friedrichroda, and various Saar-Nahe sites such as Lebach, have yielded a great number and variety of obligatory aquatic amphibians, but only very rarely terrestrial or semiterrestrial tetrapods (Milner and Panchen, 1973; Milner, 1993).

Two important conclusions have been suggested (Berman and Martens 1993; Sumida et al., 1996; Berman et al., 1997) to explain the high degree of commonality between the Bromacker tetrapod assemblage and those of the Lower Permian red-bed deposits throughout the United States: 1) similar environments, as represented by typical fluvial red-bed facies, are being sampled; and 2) an absence of major physical and biological barriers during the Early Permian allowed faunal interchange across northern Pangaea.

The striking similarities between the Bromacker assemblage and those of North America have also brought into question the widely accepted assessments of the biostratigraphic position and age of the Tambach Formation, lowermost formational unit of the Lower Permian Upper Rotliegend of the Tambach Basin in the midregion of the Thuringian Forest of central Germany. The Rotliegend, as well as its lower and upper subdivisions (in western Europe the lithostratigraphic terms Autunian and Saxonian are commonly used in place of Lower and Upper Rotliegend, respectively), is a traditional lithostratigraphic unit that refers to continental beds considered to be entirely or in great part Lower Permian and to overlie Upper Carboniferous Stephanian deposits in central Europe. In the region of the Thuringian Forest the Upper Permian marine Zechstein overlies in places the Rotliegend. Certain elements of the Bromacker assemblage, particularly *Seymouria* cf. *S. sanjuanensis*, *Diadectes*, and trematopid, strongly suggest an earliest Permian Wolfcampian age for the Tambach Formation. This, in turn, indicates that most or possibly all of the underlying Lower Rotliegend in the Thuringian Forest region should be reinterpreted as Upper Carboniferous (Berman and Martens, 1993; Sumida et al., 1996), rather than the widely accepted Lower Permian.

The following acronyms are used to refer to institutional repositories of specimens: CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; FMNH, Field Museum of Natural History, Chicago, Illinois; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; MNG, Museum der Natur, Gotha, Germany; UCMP, Museum of Paleontology, University of California, Berkeley, California.

Anatomical structures are identified by the following abbreviations: a, angular; af, anterior fenestra; ar, articular; ati, atlantal intercentrum; atn, atlantal neural arch; axc, axial centrum; axi + atp, axial intercentrum plus atlantal pleurocentrum; axn, axial neural arch; bo, basioccipital; c, coronoid; c3, centrum 3; d, dentary; ec, ectopterygoid; en, external naris; fp, footplate of stapes; i3, intercentrum 3; in, internal naris; j, jugal; l, lacrimal; m, maxilla; mf, medial fenestra; n, nasal; na4, neural arch 4; oc, occipital condyle; osp, ossified plate of stapes; ot, otic trough; p, parietal; pal, palatine; pat, proatlas; pm, premaxilla; po, postorbital; pop, paroccipital process; pp, postparietal; pra, prearticular; pro, prootic; ps, parasphenoid; pt, pterygoid; q, quadrate; qf, quadratojugal foramen; qj, quadratojugal; r1, atlantal rib; r2, axial rib; r3, r4, presacral ribs 3 and 4; sa, surangular; sf, stapedia foramen; sm, septomaxilla; sop, supraoccipital-opisthotic; sp, splenial;

sq, squamosal; ss, stapedial shaft; st, supratemporal; t, tabular; v, vomer; I–V, carpal digits.

SYSTEMATIC PALEONTOLOGY

Order Diadectomorpha

Family Diadectidae

Genus *Diadectes* Cope 1878

Diadectes absitus, new species

Holotype.—MNG 8853, greater part of an articulated skeleton with skull contained in two adjoining blocks and lacking the following: large portions of the tail; interclavicle; left shoulder girdle, forelimb, and manus; right radius, ulna, and manus; left hindlimb and pes; and most of the right pes. A disarticulated right clavicle preserved directly above the cervical vertebrae was removed. A string of four distal caudal vertebrae lying a short distance to the right of the midlength region of the presacral column almost certainly belongs to the holotype.

Paratypes.—MNG 8747, greater part of skull with lower jaws; MNG 7721 and 8978, greater portions of articulated and partially articulated, respectively, postcranial skeletons.

Horizon and Locality.—Uppermost level of 60 m-thick Tambach Sandstone of the Lower Permian Tambach Formation, Upper Rotliegend, in the Bromacker locality of the middle part of the Thuringian Forest near the village of Tambach-Dietharz and about 20 km south of the town of Gotha, central Germany.

Diagnosis.—Can be distinguished from all other *Diadectes* species by the following autapomorphic features: 1) postfrontal chevron-shaped, with its posterior apex penetrating deeply into anterior margin of parietal; 2) postorbital has very narrow entrance into orbit; 3) abrupt, dorsalward, step-like retreat of anterior portion of jugal from the free, ventral margin of the skull; 4) lower jaw subcircular in cross-sectional shape at level of coronoid eminence with the height and width being nearly equal; and 5) dentary lacks a prominent labial parapet lateral to the cheek teeth and in its place is a wide, dorsally facing platform. The following plesiomorphic features distinguish *Diadectes absitus* from all other members of the genus: 1) dorsal process of premaxilla long and narrow, extending to a level beyond the posterior margin of the external naris; 2) prefrontal extends well beyond the level of the anterior margin of the frontal; 3) postorbital forms for most of its posterior extent a tapering, triangular process that ends in a very narrow contact with the supratemporal; and 4) basicranial joint remains open and mobile in adults.

Etymology.—Latin, *absitus*, meaning distant, apart, or remote, referring to its distant occurrence from all other known members of the genus that occur in North American.

Description.—**Skull Roof**. The skull of *Diadectes absitus* conforms very closely to descriptions of North American members of this unique genus. For this reason the description that follows, including the postcranium, is mainly restricted to those features that are either at variance with previous accounts (Olson, 1947, 1950; Watson, 1954; Lewis and Vaughn, 1965; Berman et al., 1992) or are not obvious from the illustrations presented here or elsewhere of North American species. With this approach in mind, in all the figures presented here to illustrate the cranial anatomy of *D. absitus* the identification of structures has been limited mainly to those in which possible confusion may occur. In addition, cranial sutures have been drawn on the skulls with ink.

The skulls of the holotype MNG 8853 and the paratype MNG 8747 (Fig. 1–8) are approximately the same length (13.0 cm), but in other measurements, particularly transverse dimensions, the holotype is 9–12% larger. The holotypic skull is complete and has undergone minor dorsoventral crushing of the right side and occiput and lateral crushing of the left side. The paratypic skull MNG 8747, on the

other hand, has been crushed moderately dorsoventrally, and considerable amounts of bone have been lost from the cheek regions. As in the North American species, the roofing bones of both skulls are thick and porous, with a high degree of relief, particularly on the table portion, where well-developed, irregular prominences are created by a network of prominent, smooth channels or grooves. Also as in the North American species, these features are more prominent in the smaller, less mature MNG 8747 than in the holotypic skull.

The premaxillae are preserved in both skulls, but only in MNG 8853 (Fig. 3, 4) are the dorsal processes well preserved. They are narrow, tapering slightly to blunt points as they extend a considerable distance onto the dorsal surface of the skull to a level well beyond the posterior margin of the external nares. Each premaxilla possesses four procumbent, incisiform teeth which are subequal in size except for the fourth being considerably smaller. Although the premaxillary teeth of MNG 8853 are all present, only their labial surfaces are visible. In MNG 8747 only the bases of the teeth remain except in the right premaxilla, where the fully erupted third is missing the tip of the crown and only the crown of the partially erupted fourth is visible. The crowns of replacement teeth are also visible in the lingual pits of the second tooth of the right premaxilla and the first and third of the left. The teeth are distinctly procumbent and incisiform. The bases are oval in cross section with the long axis directed posteromedially, whereas the lingual surface of the distal portions are broadly concave, giving them a chisel-like appearance.

The paired nasals and frontals are narrowly rectangular and nearly equal in their dimensions. The frontals, however, are slightly shorter and gradually widen slightly posteriorly. In both skulls the great width of the parietals is due to a pronounced, well-defined rectangular lateral lappet that replaces, or represents the incorporation of, the intertemporal bone (Berman et al., 1992). In MNG 8747 a narrow, spike-like projection of the posterior margin of the parietal partially separates the tabular and supratemporal. In MNG 8853 the projection is much broader and subrectangular, but this may be due in part to crushing in the occipital region. The postparietal is a single, anteroposteriorly narrow, rectangular bone, which in MNG 8853 has a width approximately four times its midline length. Approximately one-third of the postparietal surface area, extending along its anterior margin, is exposed on the skull table, whereas the remaining posterior portion of the bone is angled abruptly downward onto the occiput to overlap the dorsal margin of the supraoccipital. In MNG 8747 the posterior portion of the postparietal slopes ventrally from the skull table at about 45°, whereas in MNG 8853 the surface is vertical. Although the prefrontal extends noticeably beyond the level of the anterior margin of the frontal in both skulls, the extension is greater in MNG 8853. The chevron-shaped postfrontal forms the posterodorsal margin of the orbit, with the posterior apex penetrating deeply into the anterior margin of the parietal.

Description of the cheek bones is based almost exclusively on MNG 8853. The postorbital has a narrow entrance into the posterior corner of the orbit. The greater portion of the postorbital forms a posteriorly narrowing, triangular process that extends along the lateral margin of the parietal lappet to within a short distance of the expanded otic, or temporal, notch. The postorbital ends in a narrow contact with the supratemporal, thus preventing contact between the lateral lappet of the parietal and squamosal. At its anterior contact with the premaxilla the maxilla has a short, narrow, dorsally directed, process-like extension that enters the external naris. Posteriorly the maxilla extends to about the level of the midlength of the orbit.

Only the dentition of the right maxilla of the juvenile skull MNG 8747 is fully exposed and well preserved, and includes 11 teeth at various stages of replacement: teeth 2, 4, 6, 7, and 9 are fully erupted, ankylosed, and show wear on the lingual cusp and on some of the central cusps as well; teeth 1, 5, and 10 are fully erupted, ankylosed, and show no wear; and teeth 3, 8, and 11 are partially erupted and not ankylosed. The crowns of replacement teeth are visible in the lingual pits of the second, fourth, and ninth teeth. The maxillary dentition is essentially identical to that of other members of the genus. Yet, a description providing some details is warranted, because *Diadectes* exhibits marked developmental growth stages of the marginal dentition that differ from those in the very closely related, Late Pennsylvanian *Desmatodon* (Vaughn, 1969, 1972; Berman and Sumida, 1995). Although all the maxillary teeth in MNG 8747 are expanded transversely, they are positioned so that the labial edge of each tooth lies well anterior to the lingual edge. The first two teeth are slightly longer and more incisiform than the succeeding maxillary teeth, giving them a morphology intermediate between those of the premaxilla and the more posterior, molar-like cheek teeth. The labial cusp is essentially absent, the posteromedial surface of the well-developed central cusp is broadly concave, and the lingual cusp is weakly developed. The crown of the third tooth is only partially erupted, but also appears to be incisiform. The remaining teeth of the series increase in size to the sixth tooth and then decrease to the end of the series. The cheek teeth exhibit the typical molar-like structure seen in other species of *Diadectes*, although their degree of development or "molarization" clearly reflects a juvenile stage of growth (Berman and Sumida, 1995). The subconical central cusps of the cheek teeth are very pro-

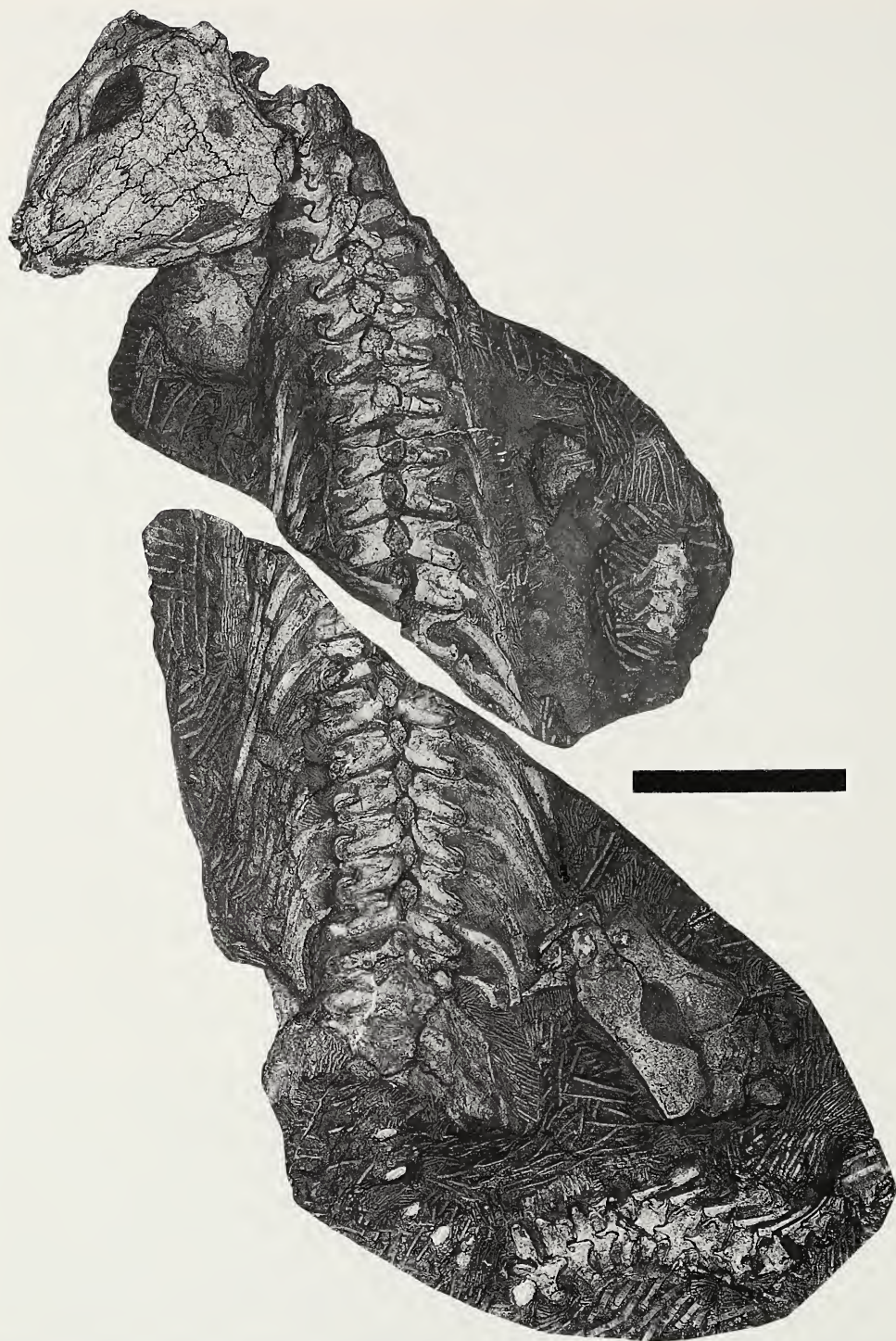


Fig. 1.—*Diadectes absitus*, holotype (MNG 8853). Greater part of articulated skeleton exposed mainly in dorsal view as preserved in two blocks and showing the skull, vertebral column except for large

nounced and represent possibly half the height of the crown, whereas the lingual and labial cusps are poorly developed and would be more accurately described as "shoulders." The lingual cusps are much more sharply defined than the labial cusps, as the bases of the central cusps are much more expanded laterally than they are medially. The sixth and largest of the molariform cheek teeth measures 7.0 mm in transverse width, 3.7 mm in anteroposterior length, and 5.0 mm in height. The spacing between cheek teeth 4 through 7 is about 1.0 mm. Enough of the right maxillary dentition of MNG 8853 is exposed laterally to indicate the presence of at least ten teeth plus spaces for two more. The teeth appear to exhibit the same serial changes as in MNG 8747.

The lacrimal and jugal are preserved only in MNG 8853. Their contribution to the suborbital bar on the right side of the skull is unusual, however, in that the suborbital process of the jugal appears to form the entire ventral border of the orbit. The typical condition for this structure is seen on the left side of the skull, where the suborbital process of the jugal is shorter, and the ventral orbital rim is completed anteriorly by a short posterior, suborbital process of the lacrimal. The jugal's contribution to the ventral margin of the skull exhibits an abrupt, step-like dorsalward retreat just anterior to the quadratojugal. This feature is especially pronounced in the left jugal.

Only the right septomaxilla of MNG 8853 is sufficiently well preserved and accessible for description (Fig. 4), and in general conforms to that described in Early Permian synapsids (Romer and Price, 1940; Wible et al., 1990). It is subrectangular in outline and lies deep within the external naris. However, because its margins are extremely thin and a major crack through the skull extends along its ventral contact with the premaxilla, the exact outlines of this element are difficult to discern. The posterior margin appears to contact the lacrimal, the dorsal margin nearly reaches the nasal, but their proximity may have been exaggerated by dorsoventral crushing of the skull, and the anterior margin ends free at about midlength of the external naris. Basically the septomaxilla is deeply bowed medially, so that its dorsal and ventral margins curve outward to the facial surface of the skull. Most prominent is a narrow, pillar-like structure, described as the dorsal process in primitive synapsids, which extends posterodorsally, joining the lateral lips of the dorsal and ventral margins of the septomaxilla. The outer surface of the dorsal process may have had a facial exposure. The dorsal process is pierced by an anteroposterior canal, the septomaxillary canal, which in primitive synapsids is believed to have transmitted branches of the superior labial nerve and artery (Wible et al., 1990). Crushing of the skull appears to have resulted in a small amount of lateral overlap of the posterior margin of the septomaxilla by the lacrimal. This may have obscured the presence of a septomaxillary foramen which is normally present at the union of the two elements.

MNG 8853 and 8747 exhibit features of the squamosal and quadratojugal (Fig. 5, 6, 7B, 9A) either overlooked or not preserved in North American specimens described by previous authors. Not mentioned in previous descriptions is a broad flange of the squamosal that projects medially and slightly posteriorly from nearly the entire length of the posterior or otic margin of its facial exposure that can be referred to as the medial flange. In MNG 8747 most of the facial exposure of the right squamosal has been lost, revealing the medial flange. It has an extensive, overlapping suture with all but a narrow ventral margin of the anterior surface of the portion of the quadrate which forms the transversely wide, anterior wall of the otic notch. In Figure 9A, however, only the lateral edge of the medial flange of the squamosal is visible. As seen in the skull MNG 8853 (Fig. 5, 6, 7B), the posterior surface of the medial flange of the squamosal is not overlapped entirely by the quadrate, and a narrow strip along its lateral margin is exposed in occipital view. Further, the facial surface of the otic margin of the squamosal is extended posteriorly 2 or 3 mm into a knife-like edge whose inner surface curves abruptly medially to become the medial flange. The quadratojugals are represented by only those in the holotypic skull MNG 8853, but only the right one is well preserved and accessible. It completes the sculptured, posteroventral rim of the otic notch, ending in a small, free, triangular, medially directed process. Below and just anterior to the sculptured medial process is a narrow, nonsculptured, sharply wedge-shaped medial extension of the quadratojugal that enters the anterior wall of the otic notch to form the medial margin of the quadratojugal foramen before ending just above the lateral condyle of the quadrate. In MNG 8747 the facial exposure of the right quadratojugal has been lost and only a broad medial flange like that of the squamosal remains. The medial flange overlaps not only the ventral margin of the anterior surface of the portion of the quadrate forming the anterior wall of the otic notch, but also the greater portion of the anterior surface of the medial flange of the squamosal.

←

portions of caudal series, iliac blades, and right tibia, fibula, and proximal portion of pes. A series of four distal caudals presumed to belong to the holotype lies to the right of the midpresacral region of column. Scale = 10 cm.



Fig. 2.—Reverse side of two blocks seen in Figure 1 containing *Diadectes absitus*, holotype (MNG 8853) and showing the skull, anterior cervical vertebrae, right femur, and puboischiatic plate in ventral view, right cleithrum and scapulocoracoid in lateral view, and right humerus with distal expansion in ventral view. Scale = 10 cm.

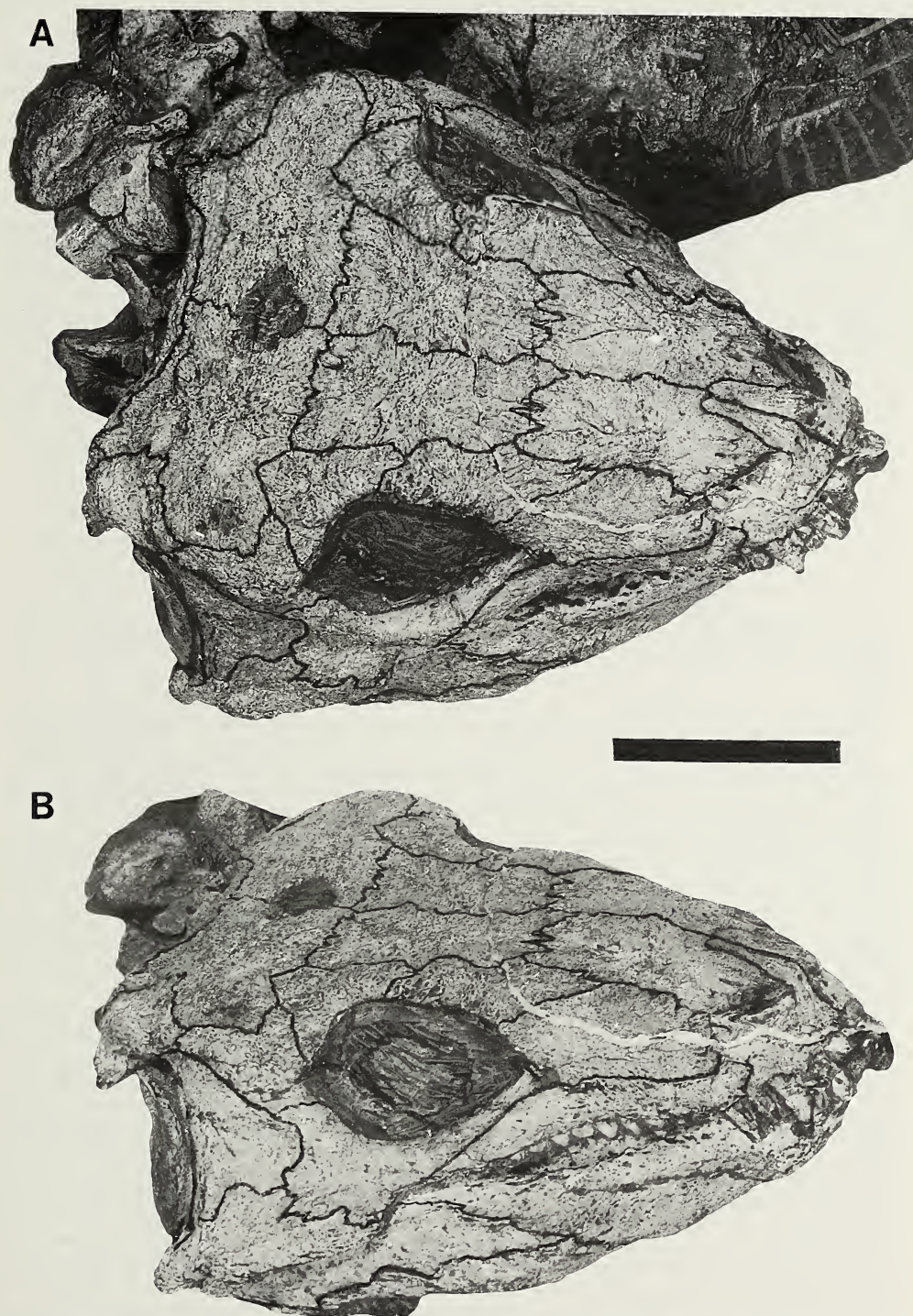


Fig. 3.—*Diadectes absitus*, holotype (MNG 8853). Skull in A, dorsal and B, lateral views. Scale = 4 cm.

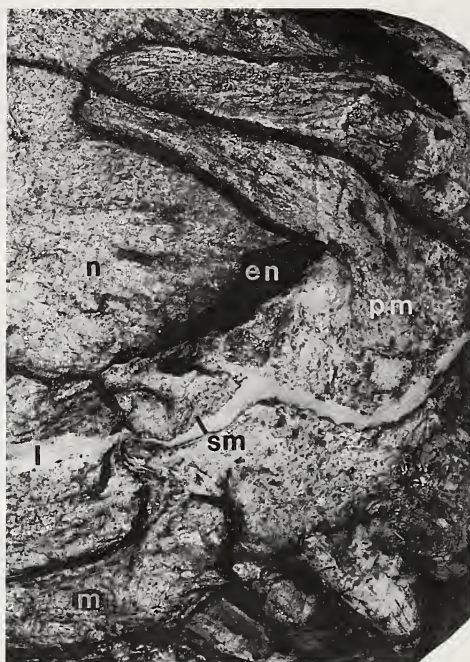


Fig. 4.—*Diadectes absitus*, holotype (MNG 8853). Right nasal region of skull in lateral view. Scale = 2 cm.

Extending posteriorly from the end of the spike-like projection of the posterior margin of the parietal is a distinct suture that continues to the distal end of the sculptured, downturned, posterolateral, horn-like extension of the skull table. This suture marks the contact between the tabular and the supratemporal. Whereas the tabular and supratemporal occupy subequal portions of the sculptured, horn-like extension of the skull table in MNG 8747, the supratemporal forms most of this structure in the larger MNG 8853. Both *D. absitus* skulls reveal that the ventral surface of the distal end of the horn-like extension of the supratemporal, that forms the posterodorsal margin of the otic notch, has a substantial contact with the dorsal edge of the distal end of the paroccipital process. From its sculptured contribution to the skull-table horn, the tabular extends medially and slightly anteriorly onto the occipital surface of the skull as a smooth plate of bone. This portion of the tabular contacts most of the dorsolateral margin of the supraoccipital–opisthotic complex of the braincase (Fig. 7B). From near the distal end of the paroccipital process, this contact arches slightly medially to reach the lateral margin of the occipital portion of the postparietal.

Palate. The palate is possibly the most poorly known region of the skull of *Diadectes*. Olson (1947) presented the most recent and detailed reconstruction of the palate, based on several individuals, yet many features remain undescribed. The palate of *D. absitus* is best preserved and exposed on the right side of skull MNG 8747 (Fig. 10), although some breakage and loss of bone has slightly obscured the sutural contacts of the palatine and ectopterygoid. In MNG 8853 the right pterygoid, ectopterygoid, and posterior half of the palatine are exposed and well preserved, as well as part of the left pterygoid (Fig. 7A). Anteriorly the vomer forms a ventrally thickened, midline, ridge-like premaxillary process that ventrally overlaps the vomerine process of the premaxilla. The premaxillary processes are very narrowly separated and their distal ends are slightly forked. Although much of the posterior contact of the vomers with the pterygoids in MNG 8747 is poorly defined, it is still traceable. Posterior to the premaxillary process the vomer continues along the midline as a dorsoventrally thickened ridge to the level of the sixth maxillary tooth and supports a single row of eight teeth. This interpretation agrees with Olson's (1947) reconstruction. From the dorsolateral margin of the premaxillary process a flat, wing-like, posterolateral extension of the vomer forms much of the anterior medial border of the long, narrow internal naris. The posterolateral wing of the vomer is not shown in Olson's (1947) reconstruction.

Anteriorly the palatal ramus of the pterygoid extends lateral to the adjacent, midline, tooth-bearing

ridge of the vomer, contacting the posteromedial margin of the posterolateral wing of the vomer. Although most of the lateral margin of the pterygoid is hidden from view by the palatine, it is clearly highly unusual in contributing to the medial margin of the internal naris, forming as much as the posterior half of the medial border of the opening, and in preventing a vomer–palatine contact. The palatal rami of the pterygoids unite along the midline for much of their length, allowing for only a short, narrow interpterygoid vacuity posteriorly. The medial tooth-bearing ridge of the vomer is continued posteriorly by the pterygoid, which contributes ten more well-developed teeth to the series. The double row of midpalatal teeth of the paired vomers and pterygoids have cylindrical bases and sharply pointed conical crowns. The teeth of both rows increase in size posteriorly from a vertical height of about 0.03 to 1.05 mm except for a marked decrease in the last three teeth. The midline vomer–pterygoid tooth rows and marginal dentitions lie at the same horizontal plane and below the slightly vaulted palatal surfaces.

The transverse flange of the pterygoid is subrectangular in ventral outline, expanding somewhat distally along its free, posterior margin. In MNG 8747 the ventral surface of the process thickens so greatly distally, that in lateral view its distal end projects well below the plane of the palate as a broadly triangular, vertical shelf (Fig. 9A). The anterior margin of the flange is defined sharply, particularly in MNG 8853, by a shallow, dorsalward, step-like elevation to the ventral surface of the palate proper. The distal half of the anterior margin of the flange contacts the ectopterygoid. In both *D. absitus* skulls the transverse flange of the pterygoid lacks teeth and, whereas the ventral surface of the process in MNG 8853 is slightly textured, that in MNG 8747 is smoothly finished. A shagreen of minute denticles is visible along the medial margin of the right palatal ramus in MNG 8747 from the base of the transverse flange to the posterior end of the medial row of teeth. The interpterygoid vacuity is closed posteriorly on either side of the midline by a very broad, posteromedially directed, flange-like process of the pterygoid, referred to here as the basal process. All but a small, triangular, anteromedial area of the ventral surface of the basal process is occupied by a slightly depressed articular facet that faces mainly ventrally and slightly posteriorly to receive the basiptyergoid process of the braincase. The quadrate ramus of the pterygoid extends posteriorly to the level of the quadrate condyle. Beginning immediately behind the transverse flange the ventral edge of the ramus forms a narrow, shelf-like lateral flange that gradually tapers posteriorly to its termination at about three-fourths the length of the ramus. A short distance posterior to the basal articulation a small, narrow, convex flange projects nearly dorsally from near the ventral margin of the central portion of the internal surface of the quadrate ramus. This flange is similar to that described in *Limnoscelis* as the arcuate flange (Romer, 1946; Fracasso, 1983).

The unique structure of the palatine in North American *Diadectes* (Olson, 1947; Berman and Sumida, 1995) is duplicated in the *D. absitus* (Fig. 7A, 10). There is a pronounced, arcuate, secondary palatal shelf that extends medially from its contact with the inner margin of the maxillary alveolar shelf and ventral to the primary palatal shelf of the true palate. In palatal view the secondary shelf partially obscures most of the contact between the primary palatal shelf of the palatine and pterygoid. A ventrally thickened, rectangular process, referred to here as the posteromedial process, extends from the posterior end of the primary palatal shelf of the palatine. Proximally the posteromedial process of the palatine nearly closes the channel formed between the primary and secondary palatal shelves of the palatine. In MNG 8747 the posteromedial process of the palatine appears to reach nearly the transverse flange of the pterygoid, whereas in MNG 8853 it is continued to the transverse flange by a short, complementary process of the pterygoid. The secondary palatal shelf of the palatine is continued a short distance posterolaterally by the ectopterygoid to the free, lateral margin of the palate. From here the shelf is continued by a short, narrow, posterior extension of the ectopterygoid that curves slightly ventrally to contact the distal end of the anterior margin of the transverse flange of the pterygoid. A small portion of the ectopterygoid posterior and medial to its contribution to the secondary palate is depressed abruptly dorsally to form a shallow concavity that is bordered medially by the posteromedial process of the palatine and posteriorly by the transverse flange of the pterygoid. In Olson's (1947:fig. 3) reconstruction of the palate of *Diadectes* he illustrated the depression at the junction of the ectopterygoid, pterygoid, and palatine as a circular pit, but noted that in some specimens this depression appears to penetrate the bone as a fenestra. Interestingly, he commented (p. 16) that the depression or pit lies in the position of the infraorbital fossa and may represent an incipient development of this opening.

Palatoquadrate. Only the quadrate (Fig. 5–7, 9, 10) of this complex has been exposed and consists basically of three major components: the condyle and two vertical sheets or laminae that arise from the condyle. One lamina, which can be referred to simply as the otic or temporal lamina, extends for a considerable height above the condyle as the transversely wide, subrectangular plate that forms the anterior wall of the otic notch. Its summit contacts the ventral surface of the supratemporal and, as shown by Watson (1954), possesses a short process at its dorsomedial margin which ends in a gently

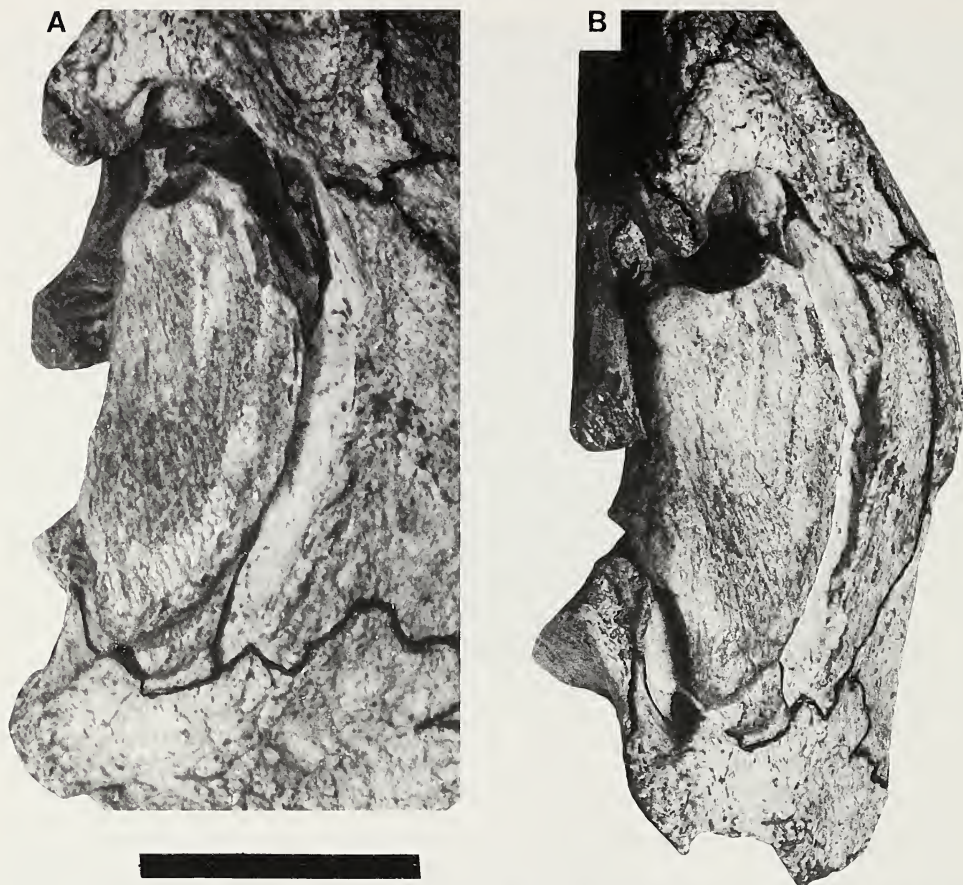


Fig. 5.—*Diadectes absitus*, holotype (MNG 8853). Right otic region in A, posterolateral and B, occipital views. Scale = 2 cm.

convex oval face that inserts into a conforming facet on the lateral surface of the prootic. At the ventromedial corner of the posterior surface of the otic lamina, just above the medial lobe of the condyle, is a short, well-defined subcircular protuberance, the quadrate boss. Lateral to the boss the quadrate forms all but the lateral margin of the quadratojugal foramen.

The second, vertical lamina of the quadrate, the dorsal process or lamina, extends anteriorly and slightly medially from the medial margin of the otic lamina, so that an approximate right angle is formed anterolaterally between them. Proximally the dorsal lamina may have reached the height of the otic lamina, but tapers somewhat anteriorly as the ventral margin of its medial surface overlaps the lateral surface of the quadrate ramus of the pterygoid. This contact is very extensive anteroposteriorly, as the dorsal lamina of the quadrate extends to approximately the level of the posterior margin of the transverse flange of the pterygoid (Fig. 9A). The greater distal portion of the ventral edge of the dorsal lamina inserts in a very shallow groove on the dorsal surface of the narrow, lateral flange of the quadrate ramus of the pterygoid.

Braincase. In MNG 8853 the only portion of the braincase visible in palatal view is the right side of the basiparasphenoid complex, whereas dorsoventral crushing has resulted in considerable telescoping and distortion of the braincase bones exposed on the occiput. On the other hand, these regions of the braincase in MNG 8747 are relatively well preserved and exposed (Fig. 9B, 10), and provide almost entirely the basis for the description that follows. The parasphenoidal rostrum is visible as a keel-like structure that extends a short distance across the interpterygoid vacuity. On the midline of its proximal end is a small, ventrally projecting protuberance. The well-developed basiptyergoid processes are subrectangular in outline, constricting somewhat at their base. They project anterolaterally

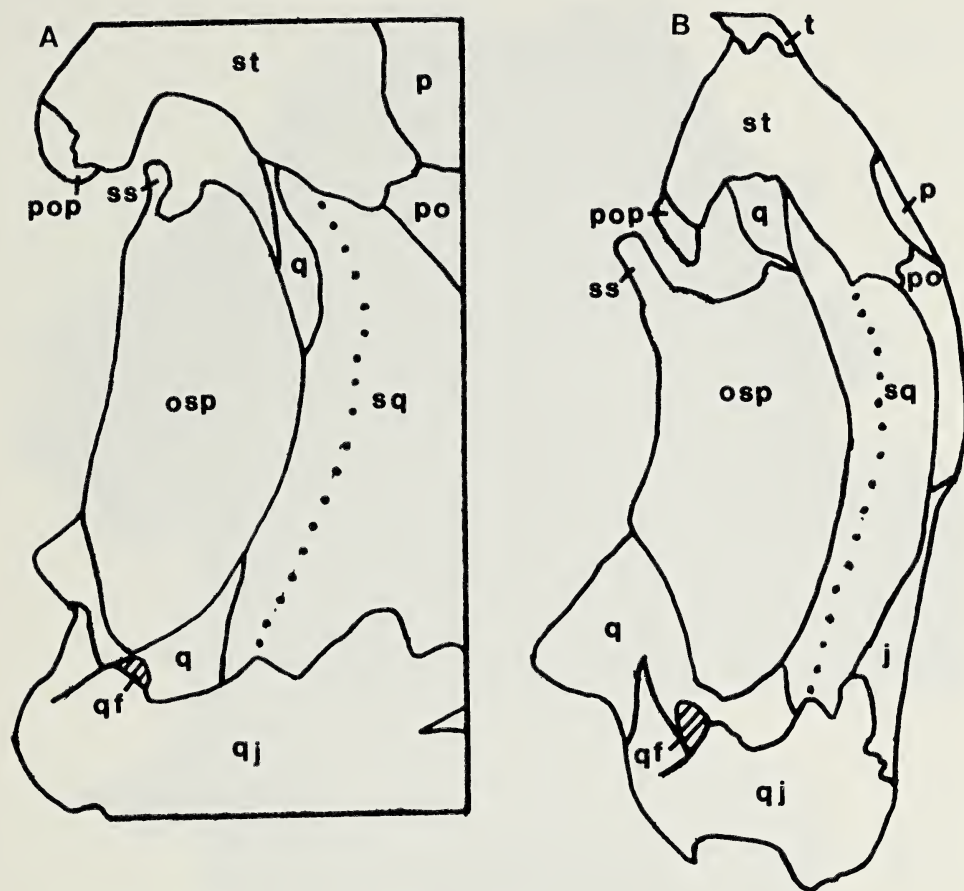


Fig. 6.—Outline sketches of views A and B of Figure 5 to indicate individual elements and other structures. Dotted line marks union of facial and occipital surfaces of squamosal.

and slightly ventrally, with their articular facets facing dorsally and slightly anterolaterally. A mobile, basicranial joint was undoubtedly present in both MNG 8747 and 8853. Posterior to the basiptyergoid processes the smooth, ventral surface of the basiparasphenoid continues a short distance before expanding on either side of the midline as thin, free-edged, ventrally arching sheets that extend posterolaterally to form long, triangular projections, the cristae ventrolaterales. A very narrow space separates the posterior edges of the cristae from the overlying basiparasphenoid complex proper which continues a short distance posteriorly to a transverse, feathered contact with the basioccipital. In both *D. absitus* skulls the occipital condyle faces strongly posteroventrally, which may be due in small part to dorsoventral crushing. In posterior view the condyle is semicircular in outline, with rounded dorsolateral corners and a slight, middorsal concavity. In MNG 8853 the articular surface is essentially flat, whereas in MNG 8747 there is a deep, central notochordal pit.

The prootics are exposed in palatal view of the skull MNG 8747 (Fig. 10). They arise anteriorly from near the base of the basiptyergoid process, with which they are indistinguishably fused, and extend posterolaterally for a considerable distance immediately adjacent to the lateral margins of the cristae ventrolaterales as wing-like sheets. Distally their incompletely preserved medial margins become very thin and appear to have ended in an abutment contact with the lateral edges of the cristae ventrolaterales. The thickened lateral margins of the prootics curve dorsally, and, although their extent in this direction can be exposed only a short distance, it is assumed that they continued as the lateral walls of the braincase. Just posterior to the palatal exposure of the right prootic in MNG 8747 (Fig. 10) is a large, stout, crescent-shaped structure that projects ventrally from near the base of the par-

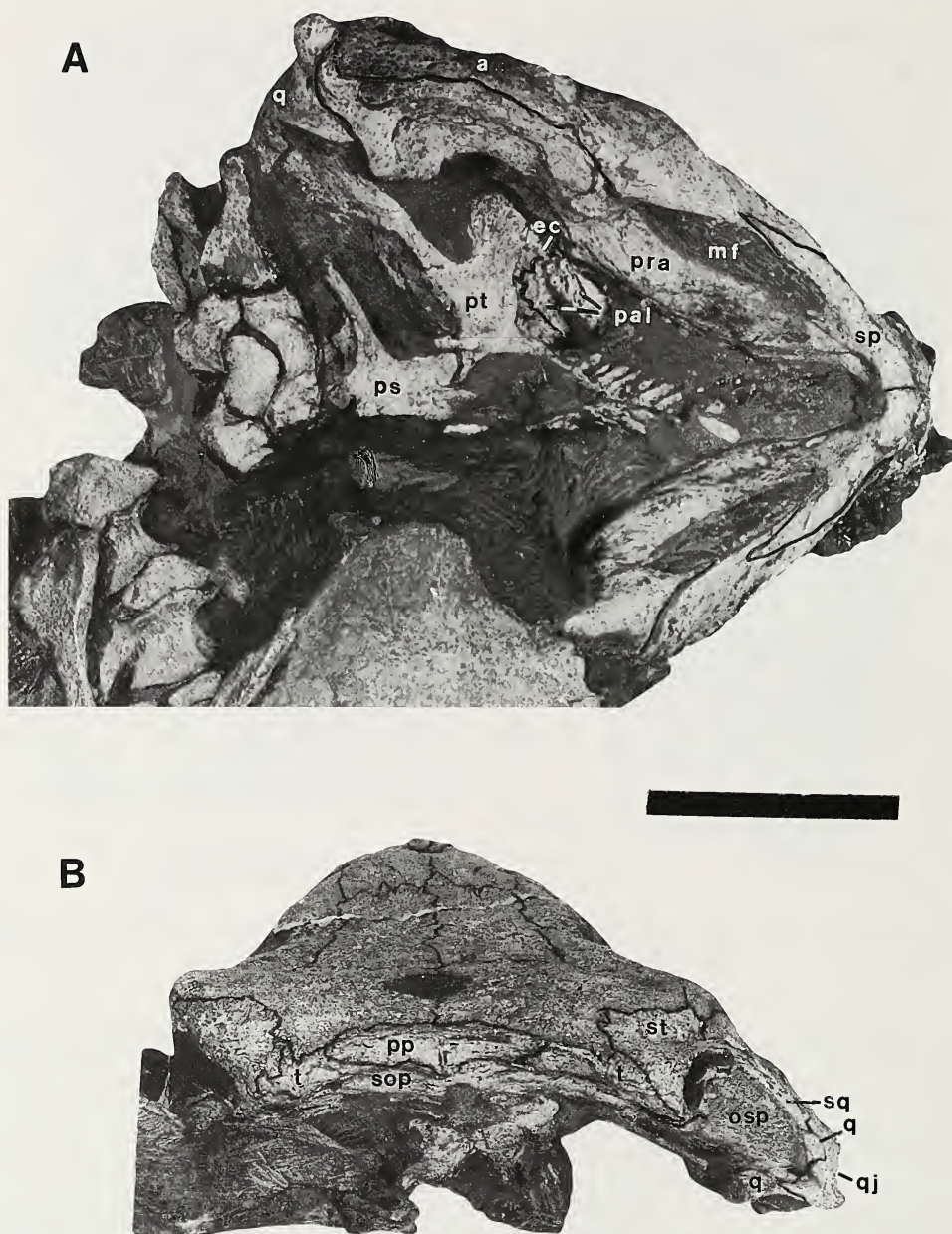


Fig. 7.—*Diadectes absitus*, holotype (MNG 8853). Skull in A, ventral and B, occipital views. Scale = 4 cm.

occipital process of the opisthotic. Its coarsely textured, concave surface faces posteromedially and ventrally. This structure, which has been termed the otic trough (Fracasso, 1983; Berman et al., 1992), has been identified in *Limnoscelis* and North American *Diadectes*, as well as in primitive synapsids, and described as being formed entirely by the opisthotic and projecting ventrolaterally from the posterior border of the fenestra ovalis (Fracasso, 1987; Berman and Sumida, 1990; Berman et al., 1992). Although a function has not been ascribed to the otic trough, the in-place exposure of the right stapes



Fig. 8.—*Diadectes absitus*, paratype (MNG 8747). Skull in dorsal view. Scale = 2 cm.



Fig. 9.—*Diadectes absitus*, paratype (MNG 8747). Skull in A, lateral and B, occipital views. Scale = 2 cm.



Fig. 10.—*Diadectes absitus*, paratype (MNG 8747). Skull in ventral view. Scale = 2 cm.

in MNG 8747 indicates clearly that the stapedial footplate articulates with the posterolateral region of its outer, convex surface.

In MNG 8747 the left exoccipital has been lost, revealing that it did not contribute to the articular surface of the condyle, but rather extended along its dorsal surface as a thin sheath flooring the foramen magnum. Immediately above its contact with the condyle the exoccipital is strongly waisted medially before continuing as a dorsomedially directed, wing-like process that borders the foramen magnum laterally. The exoccipital-opisthotic suture is quite distinct on the occiput, extending ventrolaterally onto the ventral margin of the braincase. Here it continues anteriorly, first intersecting the lateral margin of the large jugular foramen, presumably for cranial nerves IX–XI and the jugular vein, and then extends a short distance along the anteromedial basal margin of the otic trough before terminating. Although there is no visible supraoccipital-opisthotic suture, its approximate position, however, can be presumed. On the right lateral margin of the supraoccipital-opisthotic is a small opening bordered laterally by the tabular. This opening, visible on both sides in MNG 8853, is almost certainly the posttemporal fenestra, but is believed to be lost in very mature adults specimens (Berman et al., 1992). Typically in amniotes the supraoccipital-opisthotic suture extended dorsolaterally from the dorsolateral margin of the foramen magnum just above the contribution of the exoccipital to this opening and ended at or near the medial margin of the posttemporal fenestra. Immediately adjacent to and on either side of the foramen magnum in MNG 8747 is a shallow, 5 mm-long, horizontal groove occupying the presumed, approximate position of the proximal end of the supraoccipital-opisthotic contact.

Stapes. In MNG 8853 both stapes are present, but only the right is fully exposed (Fig. 5, 6, 7B), whereas in MNG 8747 only the right is present and exposed (Fig. 9A, 10). In general the stapes is divisible into two parts: an expansive, flat, distal plate that occupies the otic (or temporal) notch and a short proximal shaft with an expanded footplate. Because it could not be determined whether the distal plate represents an ossified tympanic membrane or is completely or partially stapedial, it was termed simply the “ossified plate” by Olson (1966). In MNG 8853 the ossified plate occupies nearly the entire otic notch, with its lateral perimeter reaching to within 3 or 4 mm of and paralleling the otic notch. A short, stapedial shaft projects dorsomedially from the medial margin of the ossified plate at a level about one-fourth the distance down in its height. Below the shaft the dorsal two-thirds of the medial margin of the ossified plate thickens greatly and extends a short distance as it wraps around the medial margin of the quadrate. At the base of the shaft there is a small, hemispherical swelling of the ossified plate. The bluntly pointed ventral end of the ossified plate closely approaches the small, triangular, medial process of the quadratojugal at the posteroventral margin of the otic notch. In the juvenile MNG 8747 the precursor material of the ossified plate had apparently only partially ossified, and the plate occupies only the dorsal half of the otic notch. The dorsal, or posterodorsal, and ventral margins of the plate exhibit smoothly finished edges, whereas the anterior margin is incompletely preserved. The posteroventral corner of the ossified plate thickens as it continues into the medially directed stapedial shaft. The shaft is very short and has an anteroposteriorly elongated, suboval cross section. The footplate is subtriangular in ventral view, with the posteromedial corner being greatly elongated. The medially facing surface of the footplate is slightly concave, with an irregular, roughened surface that suggests it had a cartilage covering. It is reasonable to assume that this surface articulated with the posterolateral surface of the otic trough of the opisthotic, from which it is only very narrowly separated. A small stapedial foramen pierces the posteroventral surface of the shaft.

Mandible. The greater part of the right lower jaw of MNG 8747 is preserved and has been separated from the skull (Fig. 11). It is missing large portions of the splenial, angular, and prearticular that border the medial fenestra ventrally and posteriorly, and almost the entire articular. The left jaw is very incomplete, but importantly includes the symphyseal portions of the dentary and splenial, as well as the first four teeth and the roots of the fifth and sixth. This portion has also been separated from the skull (Fig. 11E), whereas a badly damaged midlength portion remains attached to the skull. Although the lower jaws of MNG 8853 are complete, their attachment to the skull allows only partial exposures of the lateral and medial surfaces. In MNG 8747 the cross-sectional shape of the jaw posterior to the symphyseal region is subcircular, with the mediolateral width being slightly greater than the dorsoventral depth at the level of the coronoid eminence. As a result, the adductor fossa faces almost directly dorsally, and the incompletely preserved medial fossa apparently faced primarily ventrally. This arrangement nearly prevents the two openings from being visible in a single orientation of the jaw. On the other hand, in MNG 8853 jaw depth very slightly exceeds the width at the same level, and both fossae are clearly visible in medial view. These differences almost certainly reflect different ontogenetic stages.

With the exception of proportions, the lower jaw of *D. absitus* specimens deviates in only a few minor ways from those of North American members of the genus. However, because the only detailed description of a lower jaw of *Diadectes* (Welles, 1941) was based on an imperfect specimen (UCMP 33903), it is necessary to comment on some aspects of its anatomy in *D. absitus*. In lateral view of

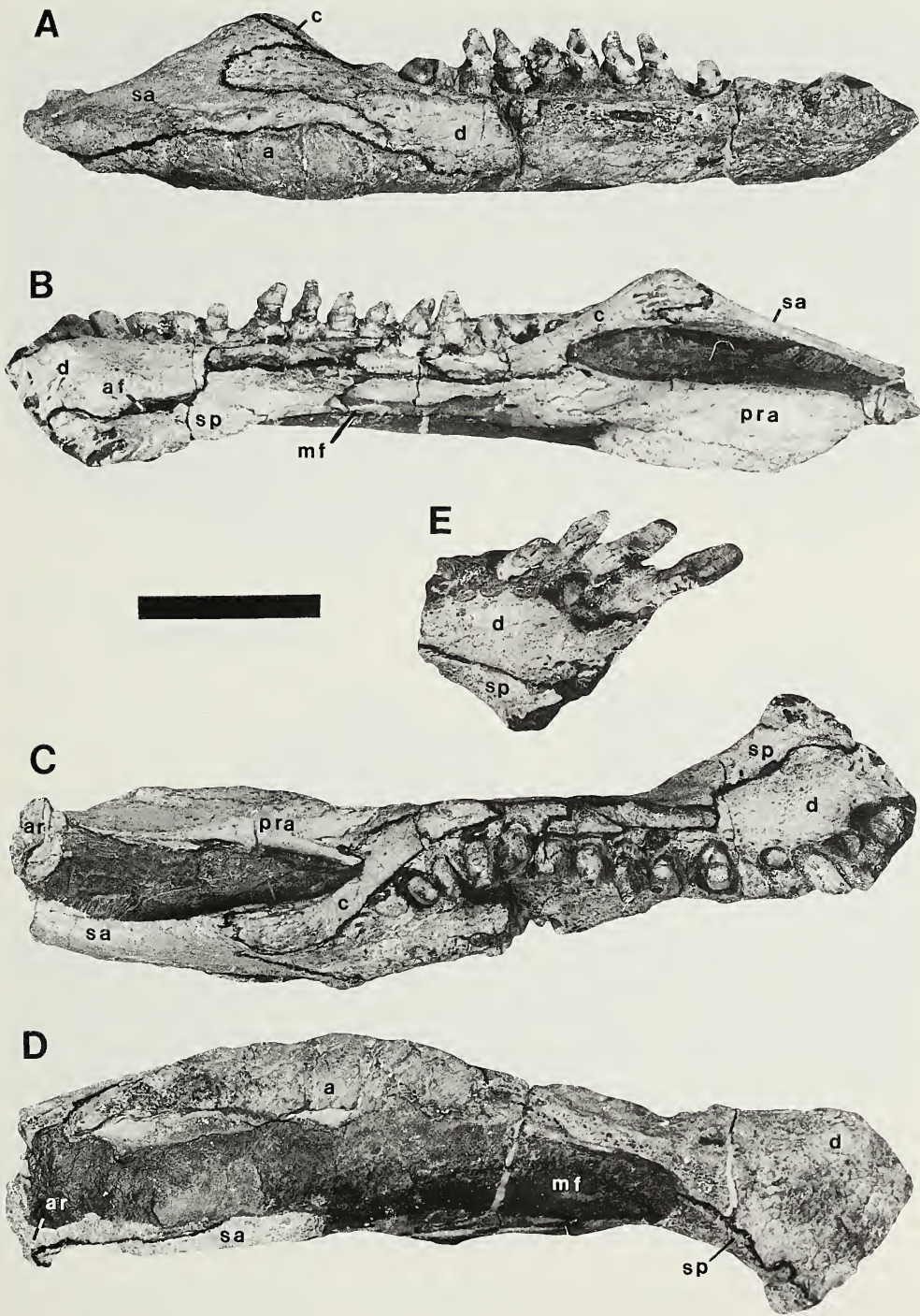


Fig. 11.—*Diadectes absitus*, paratype (MNG 8747). A–D. Right lower jaw in lateral, medial, dorsal, and ventrolateral views. E. Symphyseal region of left lower jaw in medial view. Scale = 2 cm.

the jaw the surangular tapers anteriorly along its dorsal contact with the angular as a wedge-shaped process to a level about one-fourth the distance back in the length of the angular (Fig. 11A). An unusual feature clearly visible in the right lower jaw of MNG 8747 is the formation by the dentary of a wide, dorsally facing platform lateral to the cheek teeth (Fig. 11C). This structure is also visible in the right lower jaw of MNG 8853; however, it appears to be relatively narrower and possibly bordered by a low, rounded facial ridge of the dentary.

The dentary dentition is exposed only in MNG 8747, and, as in the upper dentition, is typical of that in *Diadectes*. However, the reasons for giving the above brief account of the upper marginal dentition also apply here. The right dentary possesses 15 teeth, although only the bases of the first five, and the 13th and 15th remain; fortunately, the first four teeth of the symphyseal region of the left jaw are well preserved. The first three are distinctly procumbent and incisiform, decrease markedly in size posteriorly, are narrowly separated, and, as in the premaxillary teeth, are broadly concave on the distal portion of their lingual surface, giving them a chisel-like appearance in lateral view. The fourth tooth is smaller than the preceding tooth and intermediate in form between the anterior incisors and the succeeding molar-like teeth. The molar-like cheek teeth of the series increase in size posteriorly to the ninth or tenth, then decrease gradually to the 13th, with the last two decreasing markedly. Their degree of molar-like development clearly reflects a juvenile stage of growth (Berman and Sumida, 1995). The ninth tooth of the series measures 6.0 mm in transverse width, 3.0 mm in anteroposterior length, and 4.0 mm in estimated height (the crown is badly worn). Although transversely expanded, the labial sides of the teeth are positioned well in advance of the lingual sides. The lingual and labial cusps of the cheek teeth are poorly developed and perhaps would be more accurately described as "shoulders," whereas the subconical central cusps are well developed and account for about half the height of the crown. The lingual cusps appear to be more pronounced than those of the labial side, as the bases of the central cusps are more expanded labially than they are lingually.

The coronoid, which was absent in the *Diadectes* specimen described by Welles (1941), is well preserved and entirely exposed in the right jaw of MNG 8747 (Fig. 11A–C). The coronoid forms almost the entire coronoid eminence of the jaw, which attains a height slightly above the level of the cheek teeth. Although visible in both lateral and medial views of the jaw, the coronoid is more expansive medially and forms the anterolateral border of the adductor fossa. The coronoid eminence is much thicker transversely than the surangular portion of the adductor fossa rim. From the anterior corner of the adductor fossa the coronoid extends anteriorly as a mediolaterally flattened, narrow, rectangular plate that sheaths the medial surface of the alveolar shelf of the dentary while contacting the splenial and prearticular along its ventral margin. Anteriorly the coronoid extends to the level of the sixth maxillary tooth, although there is a small gap at about the level of the 11th tooth.

In ventral view of the mandible of MNG 8853 (Fig. 7A) the splenials are exposed in part as narrow bands extending posteriorly from the symphysis along the ventromedial margin of the jaw. At about their midlength they taper posteriorly to a sharply pointed process that penetrates the anterior end of the angular. This results in the splenial being separated from the ventral border of the medial fenestra by a narrow, marginal splint of angular. Just posterior to the symphysis on the medial surface of the right jaw of MNG 8747 the dentary–splenial suture opens narrowly for a few millimeters. The margins of the opening are smoothly rounded, giving it the appearance of a fenestra. Welles (1941) identified and referred to this opening in *Diadectes* as the anterior fenestra and described it as communicating with the Meckelian canal or, as he preferred, the primordial canal.

Axial Skeleton. The complete presacral column of MNG 8853 is visible for the most part in dorsal view (Fig. 1) and includes 21 vertebrae. The atlas–axis complex is complete, although the strong, lateral angulation of the skull to the left side of the vertebral column has resulted in the disarticulation between the atlantal intercentrum–neural arch and the fused atlantal pleurocentrum–axial intercentrum components (Fig. 12). In most of its key features the complex conforms closely with that in North American species (Sumida and Lombard, 1991). Both proatlases are exposed in dorsal view, but only the right one is well exposed and little distorted. Both contact the occiput adjacent to and at the midheight level of the foramen magnum, but it is uncertain that this represents their actual point of contact with the skull. They are disarticulated from and lie just lateral to their respective atlantal neural arch halves. The right proatlas, as seen in dorsal view, consists of two subequal parts: an expanded, subcircular anterior end from whose posterior margin projects a slightly tapering, spine-like process. The anterior expanded end is strongly inclined anterodorsally, so that its ventral surface, undoubtedly the site of an articulation facet, contacts the occiput of the skull. The spine-like posterior portion, the epiphysis, must have projected directly caudally. There is a ventral thickening at the base of the epiphysis, whose ventral surface presumably possesses a facet for articulation with the atlantal neural arch.

The atlantal neural arch halves are preserved in very nearly their correct orientation and articulation with one another, the atlantal intercentrum, and the occipital condyle of the skull. The upper halves

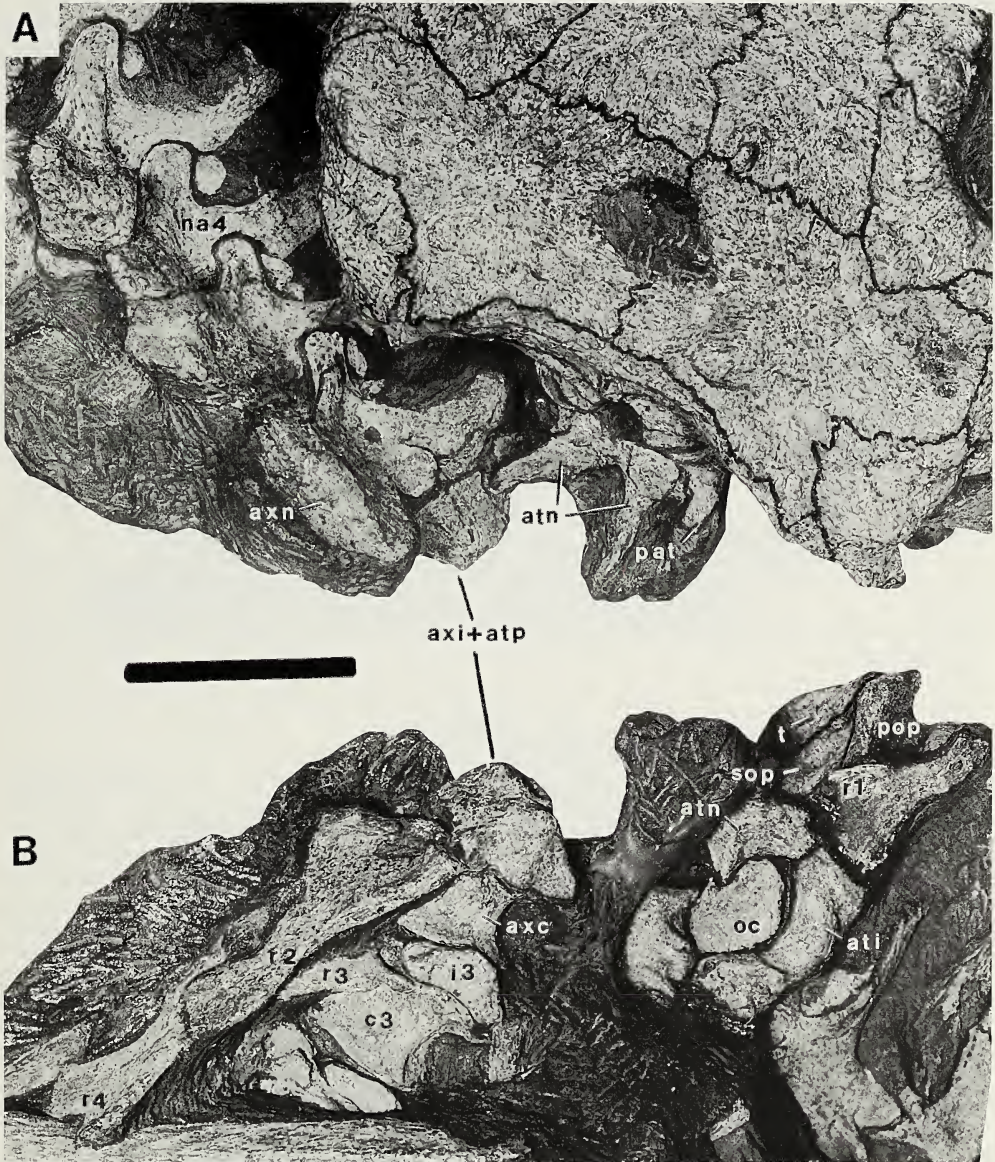


Fig. 12.—*Diadectes absitus*, holotype (MNG 8853). A. Posterior region of skull and first five cervical vertebrae in dorsal view. B. Same region as in A exposed on reverse side of block showing atlantal intercentrum and paired atlantal neural arches in posteromedial view, fused atlantal pleurocentrum and axial intercentrum in right ventrolateral view, central elements of cervical vertebrae 2–4 in ventral view, right atlantal rib in medial view, and right ribs 2–4 in lateral view. Scale = 3 cm.

of the arches are exposed in dorsal view and appear as a larger version of the proatlas. The dorsal surface of its rounded, anterior end is occupied almost entirely by a flat, anterior zygapophyseal facet for the proatlas. Medial to the facet there is a small, rectangular extension by which the arch half contacted its mate on the midline, whereas laterally (visible only on the right arch half) there is a very small triangular protuberance. Posteriorly the arch halves consist of a long, spine-like process which tapers to a sharp point and, as in the proatlas, is identified as an epipophysis. Posteriorly the

epipophyses diverge slightly from the midline. A ventral thickening at the base of the epipophysis buttresses the posterior zygapophysis. Below the level of the pre- and postzygapophyses the arch halves are visible only in posteromedial view (Fig. 12B). Each consists of a subrectangular plate with its long axis directed ventrolaterally and its internal surface facing strongly posteriorly and slightly ventromedially. The dorsomedial margins of the plates are slightly concave and diverge posterodorsally from the midsagittal plane, as they form the ventral half of the neural canal. The anterior margins clearly contacted the dorsolateral edges of the occipital condyle, whereas the ventral margins have a broad contact with the atlantal intercentrum. A short but vertically elongate diapophysis for the tuberculum of the atlantal rib projects ventrolaterally and slightly posteriorly from very low on the posterior margin of the lateral surface.

In posterior view (Fig. 12B) the atlantal intercentrum is in general crescent-shaped, with the apices of the dorsally directed lateral wings contacting the bases of the atlantal neural arches. The posterior face of the midcentral area is excavated into a broad, shallow concavity. The midventral length of the atlantal intercentrum is very short, perhaps only 2 mm. A short, vertically elongate parapophysis for the capitulum of the atlantal rib projects ventrolaterally from the lateral surface. The anterior rim of the atlantal intercentrum contacts the ventral half of the occipital condyle rim.

As previously described (Sumida and Lombard, 1991; Sumida et al., 1992) in North American *Diadectes*, the atlantal pleurocentrum in MNG 8853 is fused to the dorsal surface of the axial intercentrum. In lateral view (Fig. 12B) the pleurocentral portion has the appearance of a low, rectangular block. However, strong, laterally oblique crushing has resulted not only in some transverse narrowing of the element, but also in its right lateral surface facing ventrolaterally so as to be visible in ventral view of the complex. The flat dorsal surface of the centrum (Fig. 12A) is of unfinished bone except for a smooth, middorsal channel which ends just short of the anterior margin. The channel may represent the floor of the neural canal. These features suggest that the pleurocentrum was continued dorsally by cartilage that may have ossified later in ontogeny. In ventral view of the complex the intercentral portion has a subtriangular outline with the apex directed anteriorly and a very low, broadly rounded midline surface. The posterolateral corners are extended slightly and end in a truncated margin as the parapophyseal processes for the capitular head of the axial rib. The anteriorly directed apex is exaggerated slightly to form a bluntly rounded extension whose tip likely contacted the midventral concavity on the posterior surface of the atlantal intercentrum.

Exposure of the axis in MNG 8853 is limited to the left side of the neural arch and the right side of the centrum, and the two elements appear to be fused (Fig. 12). There is no swelling or lateral expansion of the arch, as in the immediately succeeding vertebrae. The blade-like neural spine is long and low, not exceeding the height of the more posterior spines, and thickens considerably toward its distal and posterior margins. Close to the posterior margin on the lateral surface of the spine is a well-developed, sharp-edged ridge that extends ventrally from the crest to the anterior edge of the base of the postzygapophyseal buttress. The zygapophyses are set close to the midline, although the posterior set is slightly wider apart. Whereas the anterior zygapophyses and their facets are oval, the posterior set are narrowly subrectangular. Both sets of facets slope slightly ventrolaterally. The partially exposed centrum exhibits a moderately developed midventral keel.

In MNG 8853 the intercentrum of the third cervical (Fig. 12B) is about two-thirds the size of that of the axis and is weakly chevron-shaped with the apex directed anteriorly, as reported in *Diadectes* (Sumida and Lombard, 1991). Intercentrum 4 and those of succeeding vertebrae are much smaller and have a laterally expanded oval outline.

The postaxial neural spines (Fig. 1) are low and roughly diamond-shaped in horizontal section, with the long axis oriented anteroposteriorly. They increase slightly in transverse width from the third to the seventh vertebra, becoming nearly quadrangular in horizontal section, then decrease in width gradually in the succeeding seven or eight vertebrae to a narrow diamond outline that is essentially maintained to the end of the presacral series. The summits of the spines are very coarsely textured, giving them an irregular margin. This is particularly true of those in the anterior half of the presacral series, where the summits are slightly expanded, giving the spines a slightly mushroom-like appearance. Additionally, in this region of the column there is also a bilateral constriction of the neural spine close to the posterior corner of its summit, so that in dorsal view this angle of the spine is converted into a process-like structure. A further variation in spine structure is seen in the vertebrae near the posterior end of the dorsal series in MNG 7721, where the lateral, angular margins of the spines are expanded laterally into short, irregular processes (Fig. 1, 13C). One noticeable exception to the general structure of the postaxial dorsal neural spines given above is that of the fourth vertebra in MNG 8853 (Fig. 1, 12A), which is greatly reduced in both its lateral and longitudinal dimensions to a nearly blade-like structure (a similar condition is seen in the amphibian *Eryops*; Moulton, 1974). Seemingly, longitudinal compression of this region of the column has brought the neural spines of these three vertebrae into contact.

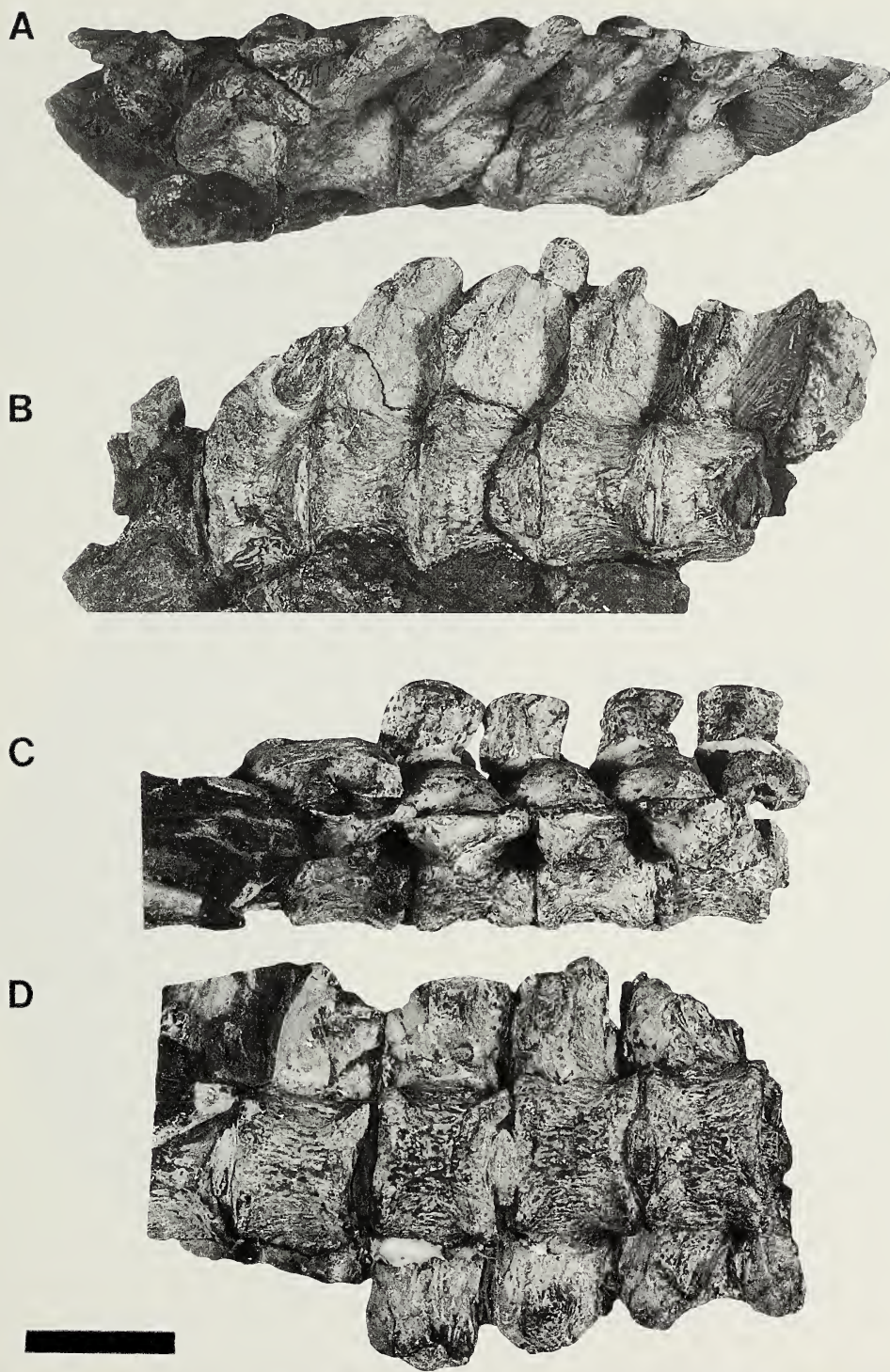


Fig. 13.—*Diadectes absitus*, paratype (MNG 7721). A, B, Postaxial cervical and C, D, posterior dorsal vertebrae in lateral and ventral views (anterior to the left), respectively. Scale = 4 cm.

The neural arches of all the presacrals of the postcervical region (Fig. 1) are swollen, with the zygapophyses extending laterally well beyond the lateral margins of the centra. In the first nine vertebrae there is a marked, successive increase in the lateral extent of the zygapophyses from very close to the midline in the atlas-axis complex to nearly equalling the lateral extent of the transverse processes. More posteriorly, the presacrals exhibit only a very gradual increase in this dimension. The low, squat structure of the presacrals is expressed particularly in the near-horizontal plane occupied by the dorsal crests of the posterior zygapophyseal buttresses. The zygapophyseal planes in the cervical region appear to slope slightly posteroventrally, whereas those of the rest of the presacrals are horizontal.

Lateral and ventral views of the presacral vertebrae have been possible only in two short series in MNG 7721 (Fig. 13): one includes five postaxial cervicals lacking mainly the neural spines and the other includes six dorsals (only five are shown) from just anterior to the sacrum. Their differences are reflected mainly in the structure of the transverse processes. In the vertebrae from the cervical region the transverse processes are laterally projecting, anteroposteriorly thin, and dorsoventrally elongate ridges. In lateral view they extend diagonally anteroventrally from the posterior surface of the anterior zygapophysis to the upper portion of the anterior centrum rim. The narrow costal facets for the ribs face ventrolaterally and slightly posteriorly and show no noticeable expansions demarking capitular and tubercular areas. In end view of the vertebrae the processes shorten gradually in lateral extent as they extend anteroventrally, but still end with a rather long, nearly horizontal ventral margin. The transverse processes in the string of posterior dorsals are thicker, project directly laterally, and are restricted to the posterior surface of the anterior zygapophyseal buttress and do not extend onto the centrum. Their wider costal facets face mainly laterally and slightly posteroventrally and are slightly constricted into nearly equal capitular and tubercular regions, the former being a little wider. Disarticulation of the last or sixth vertebra of the string of far posterior dorsals reveals the absence of hypantrum and hyposphene accessory articulations. The last two vertebrae of the string are deeply amphicoelous, but do not appear to be notochordal. In some of the vertebrae there is an indication of a neurocentral suture which may suggest a less than fully mature condition.

Except for the atlas-axis complex, the centra of the presacral vertebrae are spool-shaped, with horizontal diameters of the ends exceeding the lengths in the cervicals and farthest posterior presacrals in MNG 7721 by approximately 40 and 18%, respectively. The lateral surfaces of the centra are flared moderately outward to thickened, semicircular rim lips. Flaring of the ventral surface of the centrum is much less pronounced, and there are no midventral ridges. The midventral margin of the posterior rim of the centrum is bevelled to accommodate the small intercentrum.

All that can be seen of the two sacral vertebrae in MNG 8853 (Fig. 1) are the poorly preserved neural arches. However, a large portion of the tail of MNG 8853 is preserved (Fig. 1, 14) and includes a string of 18 vertebrae, although nine are represented only by intercentra or haemal arches. As preserved, the first five vertebrae of the series are represented by only the intercentra in dorsal view. They have a narrow, oval outline and are aligned as if retaining their original spacing and orientation. The caudal series is continued posteriorly by nine complete, laterally exposed vertebrae that diminish steadily in size posteriorly. Their neural arches are narrow, not swollen, with the zygapophyses positioned close to the midline. The anteriormost neural spine of the series curves slightly posteriorly and is blade-like for most of its length, as it terminates distally in a cap-like lateral expansion that is narrowly oval in dorsal view. More posteriorly the spines gradually straighten to a vertical orientation, decrease dramatically in size, and quickly reduce and lose the cap-like expansion at their distal end. The oval zygapophyseal planes slope steeply ventromedially. The transverse processes are exposed only in dorsal view and are positioned at about midheight on the centra and adjacent to the anterior central rim. They exhibit a marked, successive decrease in size posteriorly. In the anteriormost preserved neural arch, vertebra 6 of the series, the transverse process is rather broad and long, projects directly laterally, and narrows slightly distally along its posterior margin. By the posteriormost preserved neural arch, vertebra 14 of the series, the process is reduced to a very small, ventrolaterally projecting, triangular nubbin. The centra of this series are spool-shaped with moderately concave lateral surfaces. The lips of the central rims are laterally flared, but that of the posterior rim is far more pronounced. The ventral margins of the anterior central rims are strongly bevelled to accommodate the haemal arches. The small, proximal, intercentral portions of the haemal arches are narrowly rectangular in lateral view. As the long spines extend from the posteroventral corner of the intercentral portion they gradually double in anteroposterior width by their distal end.

Directly following the nine complete, articulated caudals the remaining, preserved portion of the tail ends in a series of four haemal arches that also retain their approximate spatial relationships and alignment with the preceding arches. Their dorsal and lateral surfaces are exposed, as well as the proximal portion of their posterior surface. Additionally, the entire posterior surface of a disarticulated haemal arch is exposed in MNG 7721. In posterior view the haemal arch is Y-shaped, with the



Fig. 14.—Incomplete tail of *Diadectes absitus*, holotype (MNG 8853; see also Fig. 1). Anteriormost and posteriormost vertebrae of series represented only by intercentra and haemal arches, respectively. Scale = 4 cm.

proximal, crescentic intercentral crosspiece spanning the ends of the two arms of the Y to enclose a triangular space. The roughened, posterodorsal articular surface of the intercentral crosspiece contacted the bevelled ventral rim of the centrum. The spine ends in a laterally flattened, blade-like structure.

An isolated string of four distal caudals with haemal arches is exposed in left lateral view a short distance to the right of the midlength region of the presacral column of MNG 8853 (Fig. 1). Their proximity to MNG 8853 and similarity to those of *Diadectes* leaves little doubt that they belong to this specimen. By way of comparison with Case's (1911) description of *Diadectes*, their serial placement is probably near caudal 25. The neural spines are very small, dorsally directed, and laterally flattened with truncated tips. The zygapophyses are set very close together, and their oval facets are inclined very steeply ventromedially. Transverse processes are absent. The lateral surfaces of the centra are moderately concave, and the ventral margin of the posterior rim is bevelled to accommodate the haemal arch. The haemal arches are shorter versions of those more anterior in the caudal series.

A complete set of presacral ribs is present and well preserved in MNG 8853 (Fig. 1), but a tightly overlapping arrangement permits adequate description of only those of the atlas and axis (Fig. 12B). The complete right atlantal rib is exposed in posterior or medial view and closely approximates its correct relationship with the atlantal neural arch and intercentrum. In this view the head and shaft, which are subequal in length, form a flat, planar surface. The broadly triangular rib head was probably dicephalous, as a weakly ossified region roughly defines a narrow gap between the well-developed capitulum and the much narrower tuberculum. The short shaft maintains a narrow width that curves slightly posteriorly to its transversely truncated distal end. The right axial rib is complete, exposed in anterior or lateral view, and nearly retains its proper association with the axis. It is essentially a larger version of the atlantal rib except for the gradual, distal expansion of the shaft to a width approximately 50% greater than its proximal end. There is a continued, progressive increase in the expansion of the rib shafts 3-7, with those of vertebrae 6 and 7 having a roughly banana-shaped outline. In the remaining presacral ribs only the dorsal margins of the tubercula are visible, and the shafts maintain a nearly constant, narrow width throughout their length. The shafts exhibit a gradual increase in length to about the 14th rib, then decrease to a length nearly equalling that of the atlantal rib. Whereas the first four ribs are only slightly curved, the succeeding rib shafts exhibit a moderate posterior curvature that becomes pronounced in the last four or five presacral ribs.

Shoulder Girdle. All the elements of the shoulder girdle are well represented except the interclavicle. In the holotype the right scapulocoracoid and cleithrum are exposed below the cervical region of the skeleton (Fig. 2, 15), whereas the right clavicle was found isolated above the cervical region and was subsequently removed (Fig. 16). In the paratypes MNG 7721 and 8778 only remnants of the articulated interclavicle, clavicles, and left scapulocoracoid are preserved (Fig. 16B).

The holotypic right cleithrum (Fig. 15) is complete, exposed in lateral view, and very nearly in its correct articulation along the anterior margin of the scapulocoracoid. The cleithrum of *Diadectes absitus* very closely duplicates that seen in North American specimens (Case, 1911; Romer, 1956). In lateral view it has a narrow, sickle-shaped appearance. The expanded, posterodorsally curving upper half of the element has separated slightly from the anterodorsal corner of the scapular blade, which it presumably overlapped laterally. The much narrower ventral stem of the cleithrum maintains a constant width as it extends ventrally, terminating at the level of the upper margin of the glenoid cavity.

As shown by the posterior view of the complete right holotypic clavicle (Fig. 16A), the stem and ventral plate meet in a sharply defined internal angle of 120°. The ventral plate is bowed ventrally, with much of the posterior portion turned upward abruptly into a high, transverse, vertical wall that quickly diminishes in height as it joins the dorsal stem. In ventral view (Fig. 16B) the ventral plate is narrow and triangular, and a smooth, narrowly triangular area of the posteromedial corner is depressed dorsally. The plate ends medially in a feathered edge. The narrow dorsal stem gradually tapers distally to a blunt point. A moderate, rounded ridge extends the entire length of the medial edge of the posterior surface of the stem. Lateral to the ridge the posterior surface of the stem forms a shallow channel that probably received the ventral stem of the cleithrum.

Although the right holotypic scapulocoracoid is complete, only the scapular blade and coracoid region anterior to the glenoid cavity are well exposed (Fig. 15). A suture cannot be found between the scapular blade and coracoid plate. The scapular blade is tall and narrow, and except for the weakly ossified, obliquely truncated anterodorsal corner, is subrectangular in outline. Most unusual, but typical of North American species (Romer, 1956), is the absence of a gradual, but pronounced posterior distal expansion of the blade. The full extent of the coracoid plate is clearly seen in MNG 7721 (Fig. 16B) by either remaining bone or lighter-colored, reduced areas of the matrix that indicate where bone had been present. The coracoid plate is strongly expanded anteroventrally into a smoothly curving, almost semicircular margin. The long, narrow glenoid cavity is essentially complete and extends directly to the posteriormost point on the margin of the scapulocoracoid. As is typical of early tetrapods, the glenoid is screw-shaped, facing posterolaterally and slightly ventrally at its anterior end and dorsally



Fig. 15.—*Diadectes absitus*, holotype (MNG 8853). Right cleithrum and scapulocoracoid in lateral view (ventral margins toward top of page) and right humerus with distal expansion in ventral view (see also Fig. 2). Scale = 2 cm.



at its posterior end. A well-developed supraglenoid buttress supports the anterior end of the glenoid. Located beneath the anterior half of the glenoid is a partially preserved deep fossa. At the anterodorsal margin and deepest level of the fossa is a remnant of the coracoid foramen.

Forelimb and Manus. The humerus is best exemplified by the right element of the holotype MNG 8853 (Fig. 15), where it is exposed with the distal expansion in ventral view. The humerus has undergone some dorsoventral crushing and erosion of the surface bone. Because the humerus conforms very closely to those described (Case, 1911; Romer, 1956; Sumida, 1997) in North American *Diadectes*, only a few minor comparisons are required. The humerus of MNG 8853 appears to differ from that of the North American species in having 1) a slightly greater development of the crest of the proximal head for the attachment of the pectoralis muscle, 2) a greater distal expansion of the supinator process so that the angle formed between it and the capitellum is greater, 3) a more strongly distally hooked ectepicondyle, 4) a more transversely expanded trochlea, and 5) a slightly greater truncation of the posterodistal corner of the entepicondyle.

The only radius and ulna complete enough to warrant description are those articulated with the right manus in MNG 7721 (Fig. 17); an incomplete left epipodial pair is preserved in MNG 8978. Seen in dorsal (= anterior) view the radius has a relatively narrow, long shaft with moderately expanded ends. The proximal end is far more expanded than the distal end, and both expansions are slightly greater on the lateral margin of the bone. For most of its proximal length the cross-sectional outline of the radius is a mediolaterally expanded oval, with the medial margin flattened and the lateral margin drawn out into a narrowly pointed edge. This outline is continued to the concave proximal articular surface, whereas the poorly preserved distal end appears to have a subrectangular articular surface with the dorsoventral dimension being slightly greater.

The ulna is essentially complete in MNG 7721 except for the loss of the olecranon process. The complete bone may have been as much as 25% longer than the radius. What remains of the sigmoid notch is well defined. The bone is dorsoventrally (anteroposteriorly) narrow and greatly expanded mediolaterally. Because the ends are much more strongly flared medially than laterally, the medial margin is deeply concave. The dorsal surface of the distal end is very slightly convex. A dorsoventrally narrow articular surface, occupying the entire end of the bone, is partially divided by a shallow excavation on the ventral surface that approximates the distal margin angulation. Both distal facets face slightly ventrally, with that for the intermedium facing slightly medially and that for the ulnare facing slightly laterally.

The manus of MNG 7721 is nearly complete (Fig. 17), and the few incomplete elements, all phalanges, can be easily restored. The carpals are well articulated with no noticeable intervening spaces, suggesting a mature stage of development. The manus is exposed in dorsal view, but with the distal phalanges of digits 1–4 hyperflexed against the plantar surface. As far as known, this is the first complete carpus of *Diadectes* to be described, and it includes the expected elements, although there is no indication of a medial centrale or a pisiform ossification. The radiale is trapezoidal in outline and very thick, with a broad, flat proximal articular surface that appears to match that of the radius. The intermedium is subrectangular, but with a wedge-shaped medioproximal extension of the deep, oval ulnar articular margin. The oval ulnare is the dominant element of the carpus. Dorsal expansion of the proximal and distal margins produces a shallow, depressed central area. The lateral or proximal centrale is pentagonal in outline, with substantial contacts with the intermedium, ulnare, and distal carpals 2–4, and its proximomedial corner contacts narrowly the radiale. A series of five distal carpals is clearly defined. Distal carpal 1 appears as a small, equilateral triangle in outline and may have been displaced slightly laterally on its contact with the first metacarpal. The second distal carpal is a narrow, proximodistally elongated oval with the proximal end being wedge-shaped. Because distal carpal 2 contacts not only nearly the entire medial margin of the lateral centrale, but also the distolateral corner of the radiale, it is suspected that it may also include or has expanded to exclude the medial centrale. Distal carpal 3 is small and trapezoidal in outline. Distal carpal 4 is basically pentagonal in outline, with a proximal angulation that wedges partially between the medial centrale and the ulnare and a broad distal margin contact with metacarpal 4. The medial angulation of the fourth distal carpal contacts the lateral centrale and the third distal carpal, and its narrow, truncated lateral margin contacts the fifth distal carpal. The small, distal carpal 5 is a proximodistally short, lens-shaped element. An unidentified, subcircular element about 8 mm in maximum diameter and partially visible between

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Fig. 16.—*Diadectes absitus*. A, B. Right clavicle of holotype MNG 8853 in posterior and ventral views. C. Incomplete left scapulocoracoid of paratype MNG 7721 in lateral view (missing portions of bone indicated by reduced matrix). Scale = 2 cm.

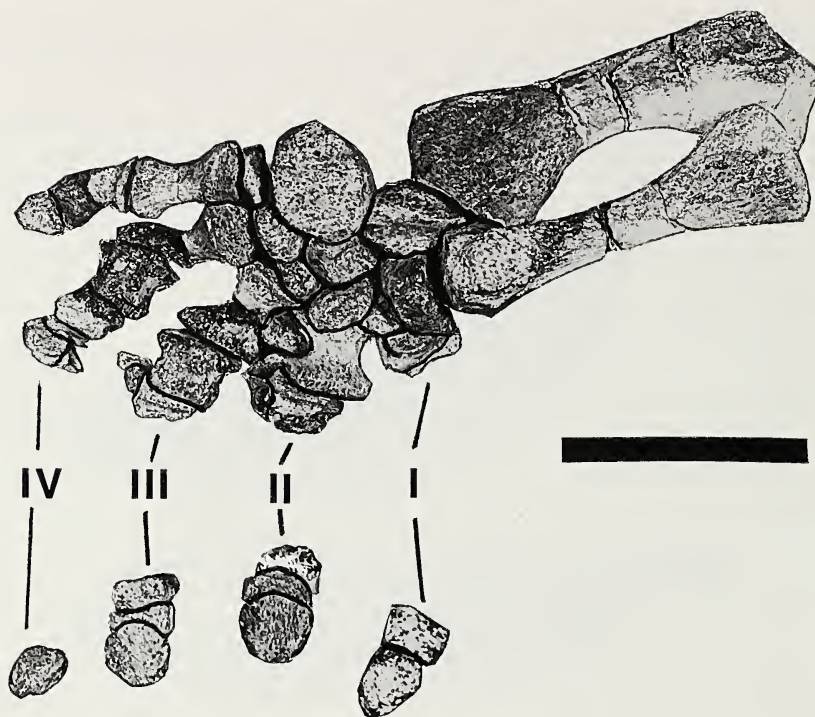


Fig. 17.—*Diadectes absitus*, paratype (MNG 7721). Articulated right radius, ulna, and manus in dorsal view. Distal phalanges of digits 1–4 are hyperflexed against plantar surface of manus and shown separately. Scale = 4 cm.

metacarpals 2 and 3 is suggestive of a carpal. Of the two carpal elements not accounted for in MNG 7721, however, a pisiform seems the most likely identification, as the tightly articulated carpus could not have accommodated a medial centrale.

Metacarpal 1 is very short and squat, whereas 2–5 are substantially larger and exhibit a gradual lengthening and narrowing serially. With two exceptions all five digits of MNG 7721 are well represented. The two phalanges of the first digit were lost due to weathering and were restored using their enclosing matrix as a natural mold to cast them in epoxy. Secondly, incomplete preservation makes it impossible to determine whether the fifth digit consisted of two or three phalanges. The phalangeal formula is, therefore, 2–3–4–5–2 or 3, but the higher count is suspected to be correct, as it is the usual formula of late Paleozoic terrestrial vertebrates. As is typical in *Diadectes*, all of the phalanges are short and broad, with the terminal ones ending in a bluntly rounded margin. An unusual *Diadectes* feature that is also present in MNG 7721 is the extreme proximodistal compression of the penultimate phalanges of digits 2–4.

Pelvis. The holotypic pelvis MNG 8853 is complete, although the ilia have suffered severe enough crushing to prevent detailed description (Fig. 1, 2, 18A). However, in MNG 8978 the disarticulated right ilium is complete and well exposed in lateral view (Fig. 18B). The anterior margin of the iliac blade is nearly vertical, with only a very slight anterodistal curvature. The posterior margin, however, is drawn out into a short, broadly triangular process that ends only a very short distance beyond the level of the expanded base of the ilium. There is no indication of an external iliac shelf, although such a structure is visible but poorly defined in the holotype. The long, quadrangular holotypic puboischiatic plate is well preserved and exposed in ventral view, with its lateral halves sloping ventromedially slightly to their midventral union to form to a modest keel. The plate is strongly waisted by the semicircular ventral rims of the acetabula, which occupy 44% of the plate's length. The union of the pubis and ischium cannot be detected, but is assumed to have occupied its normal position at about the midlength level of the acetabulum. If this is correct, the ischium is about twice the length of the pubis. Whereas the paired pubes end anteriorly in a low, triangular margin, the slightly convex posterior margins of the paired ischia form a wide, V-shaped notch in the plate. The anteroposteriorly

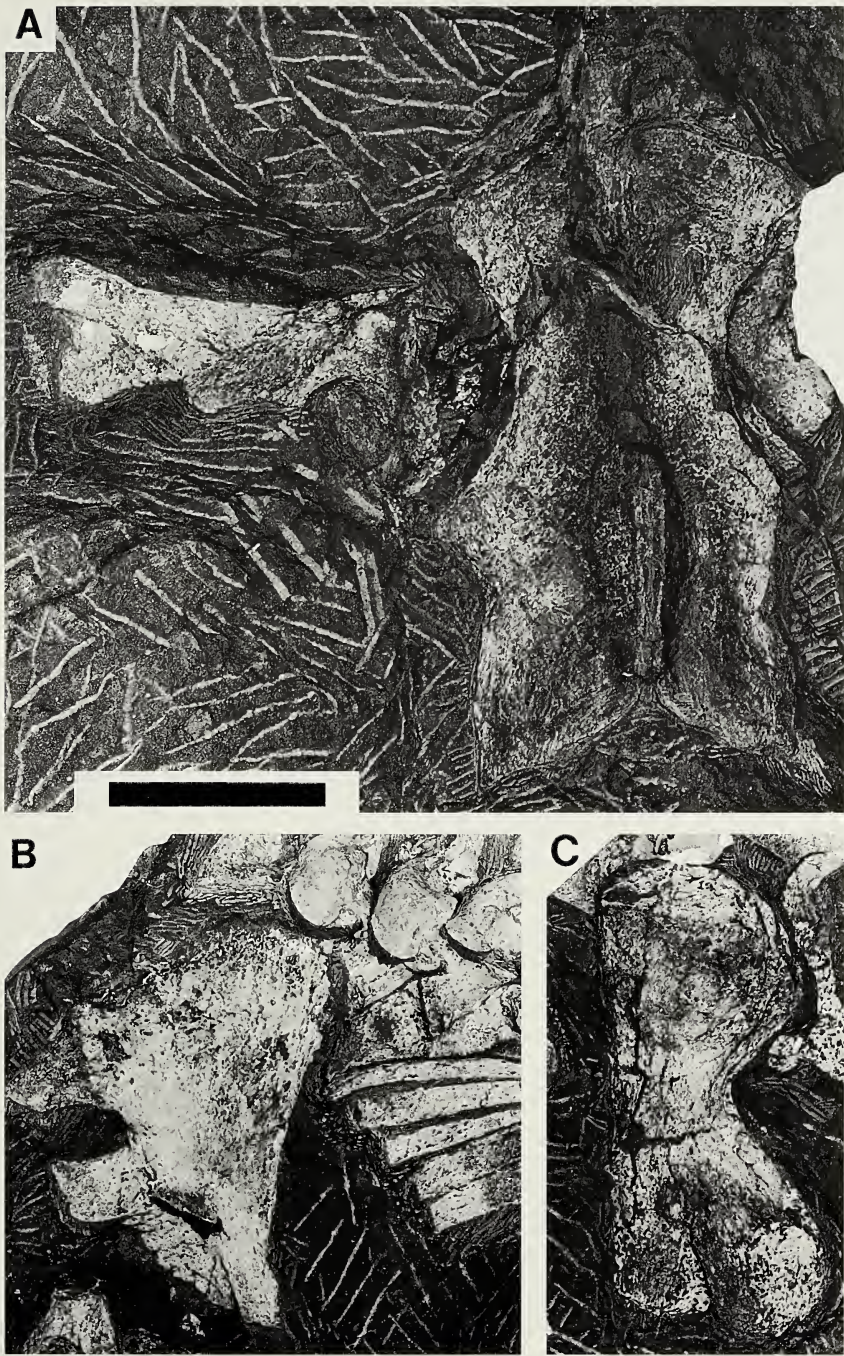


Fig. 18.—*Diadectes absitus*. A. Puboischiatic plate and femur of holotype MNG 8853 in ventral view (see also Fig. 2). B, C. Lateral view of right ilium and dorsal view of left femur of paratype MNG 8978. Scale = 4 cm.

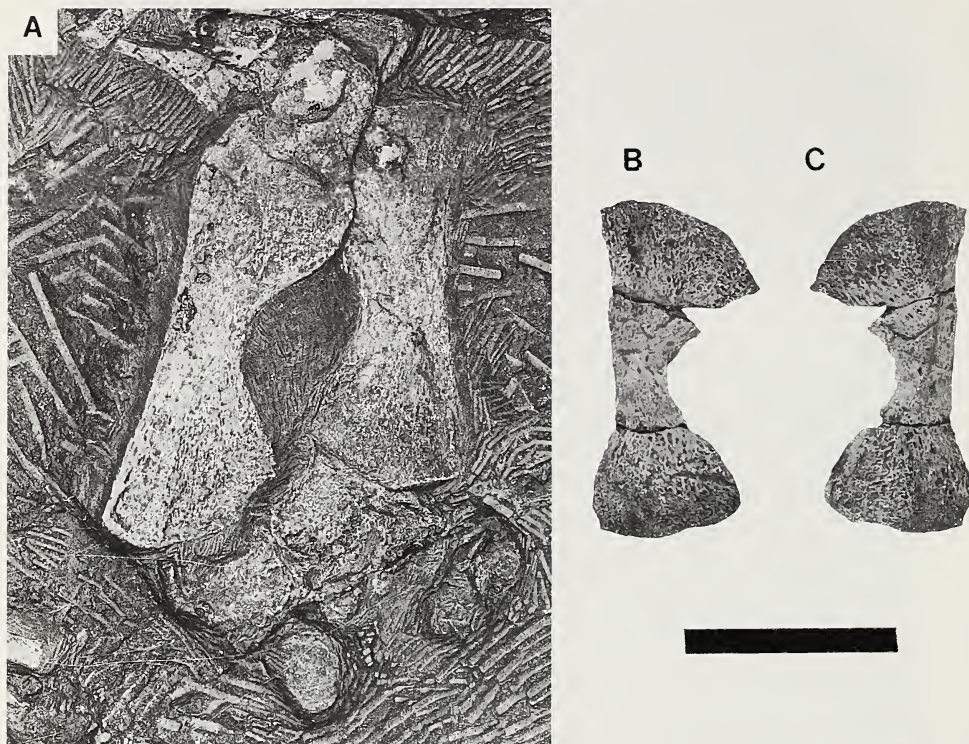


Fig. 19.—*Diadectes absitus*. A. Right tibia, fibula, and proximal portion of pes of holotype MNG 8853 in dorsal view (see also Fig. 1). B, C. Isolated left fibula of paratype MNG 7721 in dorsal and ventral views (distal end toward top of page). Scale = 4 cm.

elongate obturator foramina, defined by poorly preserved margins, lie midway between the antero-ventral margin of the acetabulum and the midventral union of the pubes.

Hindlimb and Pes. Femora are best preserved in the holotype MNG 8853 and MNG 8978, where the right of the former and the left of the latter are exposed in ventral and dorsal views (Fig. 18A, C), respectively. Both femora are complete, but the ends of MNG 8853 are not entirely exposed and those of MNG 8978 have been severely crushed dorsoventrally. The heads are widely expanded, subequal in length, and joined by a very short shaft in MNG 8853. In the smaller MNG 8978, however, there appears to be no intervening shaft. Dorsal view of the femur MNG 8978 shows the proximal and distal heads as angled posteriorly, so that the anterior margin of the bone is straight or slightly concave and the posterior margin is strongly waisted. The dorsal surface of the proximal head is broadly convex, and the narrow, terminal articular surface has a slightly crescentic outline, convex above, that thins more gradually posteriorly. As is customary, of the two distal condyles the posterior one is larger and extends a short distance farther distally. On the ventral surface of the femur MNG 8853 the depth of the intertrochanteric fossa is exaggerated along its anterior margin by a well-developed internal trochanter. The internal trochanter is continued to the distal corner of the fossa and onto the shaft, where it becomes much more pronounced as the fourth trochanter.

The best examples of the tibia and fibula are the right elements in the holotype MNG 8853 (Fig. 19A), exposed in dorsal (= anterior) view, and an isolated left fibula in MNG 7721 (Fig. 19B, C). Although other examples of these elements are present in MNG 7721 and 8978, they are too poorly preserved to be informative. Both elements in the holotype are strongly crushed dorsoventrally (= anteroposteriorly), and most of the lateral half of the proximal head of the tibia is hidden by the overlying fibula. The fibula exceeds the tibia in length by 7%. Because the ends of the tibia are much more flared laterally than medially, the lateral margin of the bone is deeply concave, whereas the medial margin is only slightly concave. Despite the extreme crushing, the cnemial crest can be seen to end proximally in a prominent, knob-like rugosity. The heads of the fibula are much more greatly

expanded medially than laterally, so that, whereas the lateral margin of the bone is only slightly concave, the medial margin is strongly concave with essentially no separation of the heads by a shaft. The proximal head terminates in a very slightly convex margin that is directed slightly posteromedially (= dorsomedially), whereas the moderately convex margin of the distal head is oriented slightly anteromedially (= ventromedially). As seen in MNG 7721, a very low ridge on both the dorsal and ventral surfaces of the distal head lies close to and parallel with the lateral margin. The ventral surfaces of both heads are broadly concave. The proximal articular surface is crescentic in outline, with the concave margin ventral, and narrows slightly from a thicker, bluntly rounded lateral margin. The distal articular surface is weakly sigmoidal, with a slight constriction dividing it into a thicker, ventrally convex medial portion for the astragalus and a thinner, dorsally convex lateral portion for the astragalus and calcaneum.

Although elements of the pes are present in the holotype MNG 8853 (Fig. 1, 19A) and MNG 7721, they are so jumbled and poorly preserved that they are of little descriptive value. The dorsal (= anterior) surface of the astragalus is, however, clearly visible in MNG 7721 (not figured) and exhibits the standard L-shaped outline. The dominant, subrectangular horizontal limb occupies about 80% of the proximodistal length of the astragalus and exceeds by 2.4 times the mediolateral width of the much smaller neck. The rectangular outline of the neck is altered by a broadly rounded proximolateral corner for contact with the fibula. At the distal end of the lateral margin opposing the calcaneum is a small, semicircular notch of the perforating foramen. A channel-like depression extends proximomedially from the foramen to the posteromedial angle of the astragalus. Just distal to the foramen the distolateral corner of the astragalus is beveled for contact with the fourth distal tarsal.

COMPARISONS AND DISCUSSION

European Diadectids

Of the vertebrates described from the Lower Permian of central Europe, only two genera can be assigned to Diadectidae with confidence, and both are from the Lower Rotliegend of Germany. On the basis of a string of six vertebrae that includes the last four presacral and two sacral from the Leukersdorf Formation of the Erzgebirge Basin near Zwickau, Meyer (1860) described *Phanerosaurus naumanni*. The vertebrae are very much like those of *Diadectes*, having very broad, massive neural arches with far laterally placed zygapophyses. A second probable diadectid was described by Geinitz and Deichmueller (1882) from Niederhaeslich near Dresden in the Doehlen Basin. They described the disarticulated remains of what they believed to be two specimens representing a new species of *Phanerosaurus*, *P. pugnax*, preserved on a series of part and counterpart slabs. These remains were more thoroughly redescribed by Stappenbeck (1905), who concluded that they belonged to only one individual. On the basis of what he interpreted as differences in their vertebrae from those of *P. naumanni*, *P. pugnax* was reassigned to a new genus, *Stephanospondylus*, and both genera were placed in the new family Stephanospondylidae. Stappenbeck's description of *S. pugnax*, which included a reconstruction of both the skull and postcranium, was strongly criticized by Romer (1925). Romer convincingly demonstrated that the remains assigned to *S. pugnax* belong to two distinct forms, a diadectid closely allied to *Diadectes* and a labyrinthodont amphibian, possibly *Onchiodon*. Those elements recognized as belonging to *S. pugnax* include upper and lower tooth-bearing jaw elements, a squamosal and articulated parietals and frontals, presacral vertebrae, expanded ribs of the subscapular region, and elements of the pectoral girdle and forelimb.

If, according to Romer (1925:458), *Stephanospondylus* is defined by the above reduced list of elements, it "emerges as a typical diadectid, differing markedly in no known character from the well-known American forms, although a more complete knowledge of the animal might show differences to be present." Stappenbeck (1905) presented a list of seven vertebral characters for distinguishing be-

tween *Phanerosaurus* and *Stephanospondylus* and on this basis established the latter genus for *P. pugnax*. Romer (1925) regarded these characters, however, as either trivial, erroneous, or of uncertain value and, therefore, as providing little basis for recognizing two genera. Again, he cautioned that the discovery of additional remains of *Phanerosaurus* may indicate its distinctiveness. Therefore, Romer recommended that the genus *Stephanospondylus* be retained for the present and, although difficult to define, offered the following characterization (p. 459): "...a small diadectid, probably about 1 meter in length, lacking a hyposphene-hypantrium articulation; the subscapular ribs, although very broad, lack the V-shaped posterior angles found in *Diadectes*; the molar teeth lack lateral cusps." The potential usefulness of this diagnosis would possibly be even further diminished if it were determined that the holotype was a juvenile specimen. The secondary vertebral articulations and the greater development of the subscapular ribs may only appear in larger, more adult individuals, where structural support is more critical; both these structures also appear to be absent in the smaller Bromacker *Diadectes*. The absence of lateral cusps on the molar-like cheek teeth in *Stephanospondylus* could also be explained as a juvenile feature. Berman and Sumida (1995) have shown that in early juvenile stages of growth the cheek teeth in *Diadectes* are bulbous and lack lateral cusps. Although weakly developed, lateral cusps are, however, present in the juvenile Bromacker *Diadectes* skull MNG 8747. Yet, the length of this skull (ca. 100 mm) is far less than that of *Stephanospondylus pugnax*, estimated by Romer (1925) on the basis of the jaw elements to be about 155 mm.

There is one other piece of evidence to suggest that *Stephanospondylus* and the Bromacker diadectid are distinct forms. In addition to the tooth-bearing jaw elements, Geinitz and Deichmueller (1882) also figured the squamosal and the articulated parietals and frontals, which were used by Stappenbeck (1905) in his reconstruction of the skull of *S. pugnax*. These elements were also suspected by Romer (1925) to belong to *S. pugnax*. The surface ornamentation on each of the parietals and frontals, however, consists of narrow ridges radiating out from a central growth region. This pattern is most like that seen in typical labyrinthodonts and quite distinct from the network of pronounced, deep, smooth, U-shaped grooves superimposed on a coarsely granular or sponge-like textured sculpturing exhibited by the skull roofing bones in *Diadectes* (Olson, 1950; Berman et al., 1992), including the Bromacker skulls. In the absence of more complete materials *Phanerosaurus* and *Stephanospondylus* should be considered as very poorly defined, although they obviously share certain features with *Diadectes*. In fact, it is suspected that further examination of the known specimens would indicate that both genera should be considered as nomina dubia.

North American Diadectes

Although there can be no doubt of the generic assignment of the Bromacker diadectid to *Diadectes*, certain problems arise when attempting to compare it to North American representatives of the genus. In a study of the systematics of Diadectidae, Olson (1947) reduced significantly the number of recognized *Diadectes* species to three, possibly four, even after synonymizing several genera with this genus. Despite a marked reduction in the number of recognized *Diadectes* species, the basis for distinguishing between the remaining North American forms relies almost entirely on the extremely questionable grounds of size, proportions,

and stratigraphic position. Further complicating the systematics of this genus are Olson's (1947, 1950) observations that individual variations within a species are often greater than those between species, the tracing of sutures of the skull roofing bones is often difficult or impossible, and proportional differences are probably often the result of differential growth rates. The lack of detailed descriptions of early growth stages of both the skull and postcranium is particularly troublesome in recognizing differences between North American species of *Diadectes* (Olson, 1947; Berman et al., 1992; Berman and Sumida, 1995). Undoubtedly due in part to these problems, the numerous descriptions and reconstructions of the skulls of North American specimens (Huene, 1913; Gregory, 1946; Olson, 1947, 1950; Watson, 1954; Lewis and Vaughn, 1965) differ strikingly and contain serious errors in interpretation (Olson, 1947; Berman et al., 1992).

Despite the above difficulties, several autapomorphic and plesiomorphic cranial characters can be recognized that distinguish *Diadectes absitus* from all North American members of the genus. Polarities have been determined using the seymouriamorph *Seymouria* and anthracosaurs as the reference outgroups for comparisons, which follows most recent studies that recognize them as the closest outgroups to the diadectomorphs (Gauthier et al., 1988; Panchen and Smithson, 1988; Berman et al., 1992; Laurin and Reisz, 1995). Most recently, however, Carroll (1995) and Laurin and Reisz (1997) have presented a radically new scheme of tetrapod relationships which recognizes the lepospondyls as the nearest outgroup of the diadectomorphs and amniotes. Because of the narrow scope of relationship being tested and of the characters being analyzed here, the alternative choice of lepospondyls as the nearest outgroup to diadectomorphs produces either ambiguous, the same, or no results. Because the Late Pennsylvanian diadectid *Desmatodon* is regarded to be a closely related predecessor of *Diadectes* (Vaughn, 1969, 1972; Berman and Sumida, 1995), it has also been included as a reference outgroup.

Dorsal Process of Premaxilla.—In *D. absitus* the dorsal process of the premaxilla is long and narrow, and extends a considerable distance onto the dorsal surface of the skull, reaching a level just beyond the posterior margin of the external naris. In all the reconstructions of North American *Diadectes* but that presented by Gregory (1946), the premaxilla is depicted as lacking a pronounced dorsal process. The presence of a well-developed dorsal process in the more primitive *Desmatodon* (Berman and Sumida, 1995), as well as in *Seymouria*, suggests that this is a plesiomorphic feature of *D. absitus*.

Anterior Extent of Prefrontal.—The prefrontal in *D. absitus* extends well beyond the level of the anterior margin of the frontal, whereas in North American *Diadectes* the prefrontal and frontal end anteriorly at approximately the same level. Inasmuch as a prefrontal extending beyond the anterior margin of the frontal is also seen in *Seymouria* and anthracosaurs, this feature is considered as plesiomorphic in *D. absitus*.

Shape of Postfrontal.—The postfrontal of *D. absitus* is chevron-shaped, with its posterior apex penetrating deeply into the anterior margin of the parietal. This configuration is due in part to a greater lateral extension of the postfrontal along the posterior margin of the orbit. In contrast, this element in North American *Diadectes* is generally subrectangular except for a lateral incision by the orbital rim and has a straight or slightly posteriorly convex line of contact with the parietal. As the shape of the postfrontal in *D. absitus* is not seen in other late Paleozoic tetrapods, its presence in *D. absitus* is judged an autapomorphy.

Shape of Postorbital.—Typically the postorbital in North American *Diadectes* is shown as having a subrectangular outline, with a broad entrance into the orbit and a broad contact with the supratemporal. In *D. absitus*, however, the postorbital has a very narrow entrance into the orbit (due partly to the encroachment of the postfrontal) and forms for most of its posterior extent a tapering, triangular process that ends in a narrow contact with the supratemporal. By way of comparison with other late Paleozoic primitive tetrapods, the restricted entrance of the postorbital is considered an autapomorphic feature in *D. absitus*, whereas its posteriorly narrowing, triangular shape is judged as plesiomorphic. In view of the fact that early tetrapods lack a postorbital–supratemporal contact, the narrow contact of these two elements in *D. absitus* is judged a plesiomorphic character relative to the broad contact in North American representatives of this genus.

Ventral Margin of Jugal.—The abrupt, dorsalward, step-like retreat of the anterior portion of the jugal's contribution to the ventral margin of the skull in *D. absitus* is considered an autapomorphic feature. Among late Paleozoic tetrapods the ventral margin of the jugal either arches smoothly anterodorsally, as in North American species of *Diadectes*, or is straight.

Basicranial Joint.—The basicranial joint in anthracosaurs, *Seymouria*, *Desmatodon*, and immature specimens of North American *Diadectes* is obviously open and mobile, whereas in mature North American specimens of *Diadectes* the joint is firmly fused (Olson, 1947; Vaughn, 1972; Berman and Sumida, 1995). Although it is not unexpected that the basicranial joint is open and mobile in the juvenile specimen of *D. absitus* (MNG 8747), the retention of this feature in the adult Bromacker specimen (MNG 8853) can only be considered as a plesiomorphic state.

Cross-sectional Shape of Lower Jaw.—In *D. absitus* the lower jaw is subcircular in cross section for much of its length. At the level of the coronoid eminence in MNG 8747 the mediolateral width of the lower jaw is slightly greater than the dorsoventral depth, whereas in MNG 8853 the reverse is true. In contrast, the lower jaws of North American *Diadectes* are extraordinary for their exaggerated vertical expansion not only at the level of the coronoid eminence, but throughout almost their entire length. As examples, the lower jaws of *D. sanmiguelensis* (MCZ 2989), *D. lentus* (FMNH UC 675), *D. lentus* (UCMP 33903), and *Diadectes* sp. (UCMP 59023), which have lengths of 8.8, 13.2, 16.0, and 25.5 cm, respectively, the depth exceeds the width by about 2.7 times at the level of the coronoid eminence. The value for this ratio for the lower jaw of *Desmatodon hesperis* (CM 47670), measuring 12.0 cm in length, is about 1:2.2 and, therefore, more closely approaches the value for North American *Diadectes* than *D. absitus*. In anthracosaurs (Panchen, 1970) the depth-to-width ratio at the level of the coronoid eminence undoubtedly approaches that in North American species of *Diadectes*, although rough estimates of the value of this ratio in *Seymouria sanjuanensis* specimens CM 28596, 28597, and 38022 is only about 2.0. This survey suggests that the relatively low, approximately 1:1 depth-to-width ratio of the lower jaw in *D. absitus* should be judged as an autapomorphic character.

Labial Parapet in Lower Jaw.—In North American species of *Diadectes*, including early growth stages, and at least mature specimens of *Desmatodon*, there is lateral to the bases of the cheek teeth a shallow groove whose outer wall is formed by a vertical extension of the lateral surface of the dentary into a low, thin ridge or labial parapet (Welles, 1941; Lewis and Vaughn, 1965; Berman and Sumida, 1995). Among Paleozoic tetrapods a labial parapet of the dentary is

unique to the North American diadectids *Diadectes* and *Desmatodon*. Although the lower jaws of both the juvenile and adult *D. absitus* specimens MNG 8747 and 8853 lack a labial parapet of the dentary, they possess in its place the equally unique feature of a wide, flat, dorsally facing platform lateral to the cheek teeth. Because of the likelihood that these two features are functionally related, the combined characters of an absence of a labial parapet and the presence of a wide, dorsally facing labial platform is judged an autapomorphy of *D. absitus*.

The above combination of autapomorphic and plesiomorphic characters of *Diadectes absitus* provides a much broader basis for defining this species than is available for distinguishing between those of North America. The greater uniqueness of *D. absitus* may reflect its wide geographic separation from the North American species. On the other hand, its greater primitiveness reinforces the assessment, reached previously on the basis of the character of the entire Bromacker assemblage (Berman and Martens, 1993; Sumida et al., 1996), that the biostratigraphic position and age of the Tambach Formation, lowermost formational unit of the Upper Rotliegend, should be considered earliest Permian Wolfcampian.

Contradictory Descriptions

There exist at least two sources of important, misleading information about the anatomy of the North American species of *Diadectes* that contradict the description given here for *D. absitus*. In a recent redescription by Berman et al. (1992) of the skull of North American *Diadectes*, based almost entirely on a single specimen (CM 25741), the temporal region was misinterpreted. Most importantly, in their description the supratemporal was mistakenly interpreted to have an extensive, medially directed occipital expansion that contacted broadly the lateral and posterior margins of the postparietal as it extended to within a short distance of the skull midline. Further, whereas the supratemporal was correctly shown as forming almost the entire posterolateral, horn-like extension of the skull table, the tabular was incorrectly shown as a very small element occupying a position medial to the distal end of the skull table extension and as incorporated into the occipital plate. This sutural pattern, considered an autapomorphy of *Diadectes* (Berman et al., 1992), falsely depicted the supratemporal as not only separating widely the parietal and tabular, but also the postparietal and tabular. This error was revealed not only by examination of the *D. absitus* skulls, but the skull of the small, juvenile, holotypic skeleton of *D. sanmiquelensis* (MCZ 2989) described by Lewis and Vaughn (1965) from the Early Permian Cutler Formation of Colorado (not available until this study). The temporal region in the North American *Diadectes* is reinterpreted here as identical to that in the German specimens. This revision, however, does not alter the analysis of the interrelationships of the diadectomorphs presented by Berman et al. (1992).

There are also several features of the postaxial presacral vertebrae of *D. absitus* that may appear to differentiate it from North American species. These differences are most likely the result of proportional growth changes, as almost all the illustrations and descriptions of North American species are based on much larger and, therefore, undoubtedly more fully mature specimens than those known from Germany. The most noticeable among these differences include: 1) in *D. absitus* the neural spines are much lower; 2) the crests of the posterior zygapophyseal buttresses occupy a nearly horizontal plane in *D. absitus*, whereas in North American species the buttresses slope ventrally at about a 25° angle from the horizontal;

and 3) hypantrum and hyposphene accessory articulations are, as far as can be determined, absent in *D. absitus*. That the above vertebral features of *D. absitus* may reflect an early adult stage of growth is suggested by their occurrence in a comparably sized juvenile or subadult specimen of *Diadectes* (CM 38036) from the Lower Permian (Wolfcampian) Cutler Formation of north-central New Mexico. Using the greatest transverse width of the presacral vertebrae (distance between ends of the posterior zygapophyses) as a means of comparison, the 5-cm measurement of the North American specimen is approximately only one centimeter narrower than those in the German specimens MNG 8853 and 7721. The North American specimen (CM 38036), however, possesses one prominent feature of the presacral column not seen in the German specimens, the alternation in height and structure of the neural spines (Sumida, 1990). This feature is common among late Paleozoic tetrapods, but in at least one form, the large captorhinid *Labidosaurus*, both morphotypes occur (Sumida, 1987, 1990). It was suggested (Sumida, 1987) that the variability of this feature in this genus might represent either a sexual dimorphic or a specific difference.

New Autapomorphies of Diadectes

In the course of describing the Bromacker *Diadectes* two additional cranial autapomorphies of this genus have been identified in addition to those recognized by Berman et al. (1992) that appear to set it apart from other diadectomorphs: 1) the palatal ramus of the pterygoid not only makes a substantial contribution to the posterior medial border of the internal naris, but also prevents a palatine-vomer contact; and 2) the supratemporal has a broad contact with the dorsal margin of the paroccipital process of the opisthotic of the braincase. Inadequate materials prevent determining the presence or absence of the above autapomorphies in the very closely related, nearly identical Late Pennsylvanian *Desmatodon*. These autapomorphies further strengthen the conclusion of Berman et al. (1992) that the highly derived nature of the genus *Diadectes* makes it the least desirable member of the diadectomorphs as a potential outgroup in phylogenetic analyses of the interrelationships of amniotes.

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NEW SPECIES OF *CERNOTINA* ROSS (INSECTA: TRICHOPTERA: POLYCENTROPODIDAE) FROM THE AMAZON BASIN IN NORTHEASTERN PERU AND NORTHERN BRAZILJAN L. SYKORA¹

Research Associate, Section of Invertebrate Zoology

ABSTRACT

Four new species of *Cernotina*—*C. harrisi*, *C. nigridentata*, *C. aestheticella*, and *C. ecotura*—are described from light-trap samples collected in the upper Amazon region in Peru and Brazil. *Cernotina bibranchiata* Flint and *C. cygnea* Flint are reported as new records for Peru. In addition, new figures of male genitalia of *C. spinigera* Flint are provided.

KEY WORDS: *Cernotina*, Trichoptera, microcaddisflies, Amazon, systematics

INTRODUCTION

This contribution is based on two collections in the upper Amazon River basin in Peru and Brazil by Dr. L. J. Davenport from Sanford University, Birmingham, Alabama, and by Dr. Jan Wilt and George Henrych from Boa Vista, Brazil, and Pittsburgh, Pennsylvania, respectively. The microcaddisflies from the Peruvian collection were studied previously by Harris and Davenport (1992). The samples available to us were collected in the vicinity of the Explorama Lodge located approximately 50 km NE of Iquitos on the Río Yanomono, just upstream from its confluence with the Amazon or Marañon (3°23'S, 72°52'W). The second locality in Peru was the Explornapo Camp located about 70 km NNE of Iquitos (3°10'S, 72°54'W) on the Río Sucusari. The area could be described as tropical floodplain forest with water levels fluctuating up to 10 m per year (Harris and Davenport, 1992). Additional light-trap samples were collected in Brazil by Dr. Jan Wilt and Mr. George Hendrych in Estado Roraima in the vicinity of Ecotur Park on Río Aqua Boa do Univini and in Boa Vista at Río Branco.

This publication deals with the genus *Cernotina* originally described from North America but recorded also from Central America, West Indies, and South America including Argentina (Flint, 1972, 1974, 1983). A high diversity of closely related *Cernotina* species has been reported from the Amazon Basin indicating that this region is the center of evolution of this genus (Flint, 1971). Therefore, it is not surprising that *Cernotina* was the dominant macrocaddisfly genus in the samples from Peru and Brazil. The collections contained a total of eight species including four previously described by Flint (1971). The type material of the four new species described in this paper is deposited in the Carnegie Museum of Natural History, Pittsburgh, Pennsylvania.

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SYSTEMATIC ENTOMOLOGY

Cernotina harrisi, new species

(Fig. 1-3)

Diagnosis.—This species is characterized by a combination of features found in male genitalia. These include wide anterodorsal aspect of segment X tapering to a split posterior section with obliquely truncate apices; short, stout dorsolateral lobe of preanal appendages with robust black, pointed apex directed ventromesad, and a second similarly shaped process located in the center of mesal margin and extended anteromesad.

Description.—Male: length 3.9 mm. Legs and antennal segments yellowish, rest of the body yellow brown. Wings venation and general structure typical for genus. Ninth abdominal segment produced anterolaterally, lateral view triangular, dorsal aspect broad, lateral margins with slight indentations, posteroventral margins deeply incised with rounded posterolateral sections. Segment X partially inserted into segments IX and VIII, in dorsal view triangular with lightly sclerotized, anterodorsal section deeply incised forming blade-like anterolateral processes, broad and bulbous midsection tapering posteriorly to a long apical lobe divided by a mesal split into obliquely truncate apices bearing several spines on mesal margins; lateral view semicircular with slightly undulate ventral margins. Dorsolateral lobe of preanal appendages stout, roughly triangular, shorter than segment X, with broad midsection tapering into pointed, black apex angled sharply ventromesad, center of mesal margin produced into distinct, large, black, pointed process extended anteromesad; lateral view of ventromesal lobe triangular and produced posteriorly into rounded apex with a row of spines on posterior margin. Inferior appendages elongate, rectangular, with rounded apex slightly curved ventrad, anterodorsal lobe long, in lateral view sinuous and sickle-shaped, ventral view of apical section curved laterad with a row of setae mesally; posteromesal lobe short and round with dark, apically pointed process directed mesad. Phallus slender with internal structure obscure but with a pair of dark internal spines.

Remarks.—This species seems to be closely related to *C. nigridentata*. Both species have the short dorsolateral lobe of the preanal appendages produced into a dark apical tooth and a ventromesal, black, pointed projection centered on the ventral margin. Both species can be separated easily by the shape and size of the posteromesal lobe of the inferior appendages which in *C. nigridentata* is well developed and longer than the main body of the inferior appendages. Based on the available material, this species is the most common *Cernotina* in the vicinity of Explorama Lodge and Explornapo Camp.

Type Specimens.—Holotype, male, Peru: Departamento Loreto, bank of Río Yanomono just below Explorama Lodge, 10 January 1993, L. J. Davenport. Paratypes, same data as holotype, 12 males; Peru: Loreto, Edge of quiet backwater adjoining Explornapo Camp, 15 January 1993, L. J. Davenport, 27 males.

Etymology.—Named for Dr. Steve Harris who provided the specimens for the species described in this paper.

Cernotina nigridentata, new species

(Fig. 4-6)

Diagnosis.—This species is characterized by the dorsal lobe of preanal appendages with prominent, black, apical and ventromesal projections; broad, undivided segment X, and by a long blade-like apicommesal process of the inferior appendages extending beyond apex of the main lobe.

Description.—Male: length 3.5 mm. Legs and antennae yellow; thorax, abdomen, and wings brownish. Wing venation and general structure typical for genus. Ninth segment in lateral view triangular with rounded anterior margin, central section of posterior margin produced in a rounded lobe providing support for the inferior appendages. Dorsal aspect of segment X bulbous with broad and inflated anterior part tapering to short and truncate apex composed of ventral, small, bilobed and membranous

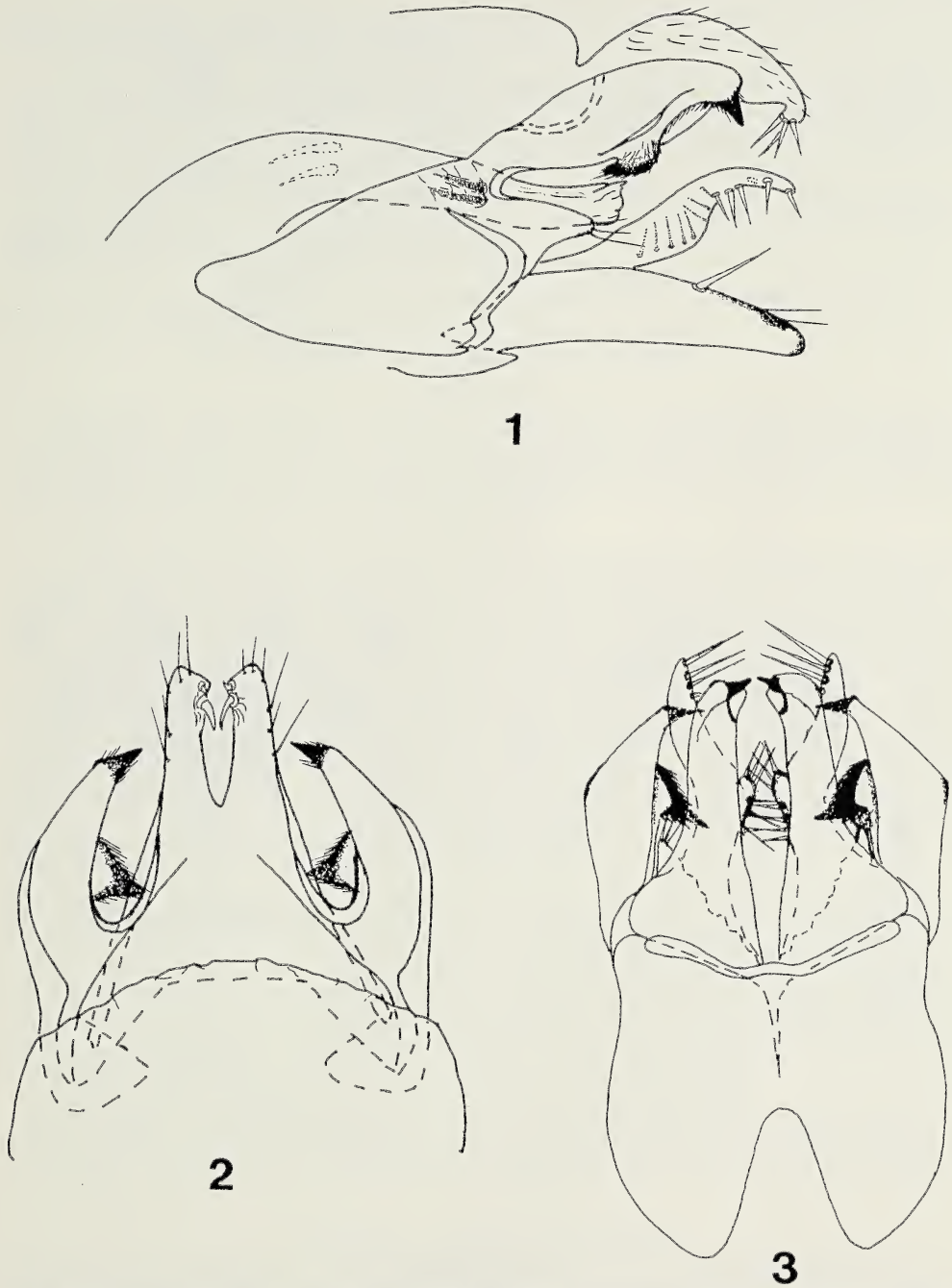


Fig. 1-3.—*Cernotina harrisi*, new species, male genitalia; 1, lateral view; 2, dorsal view; 3, ventral view.

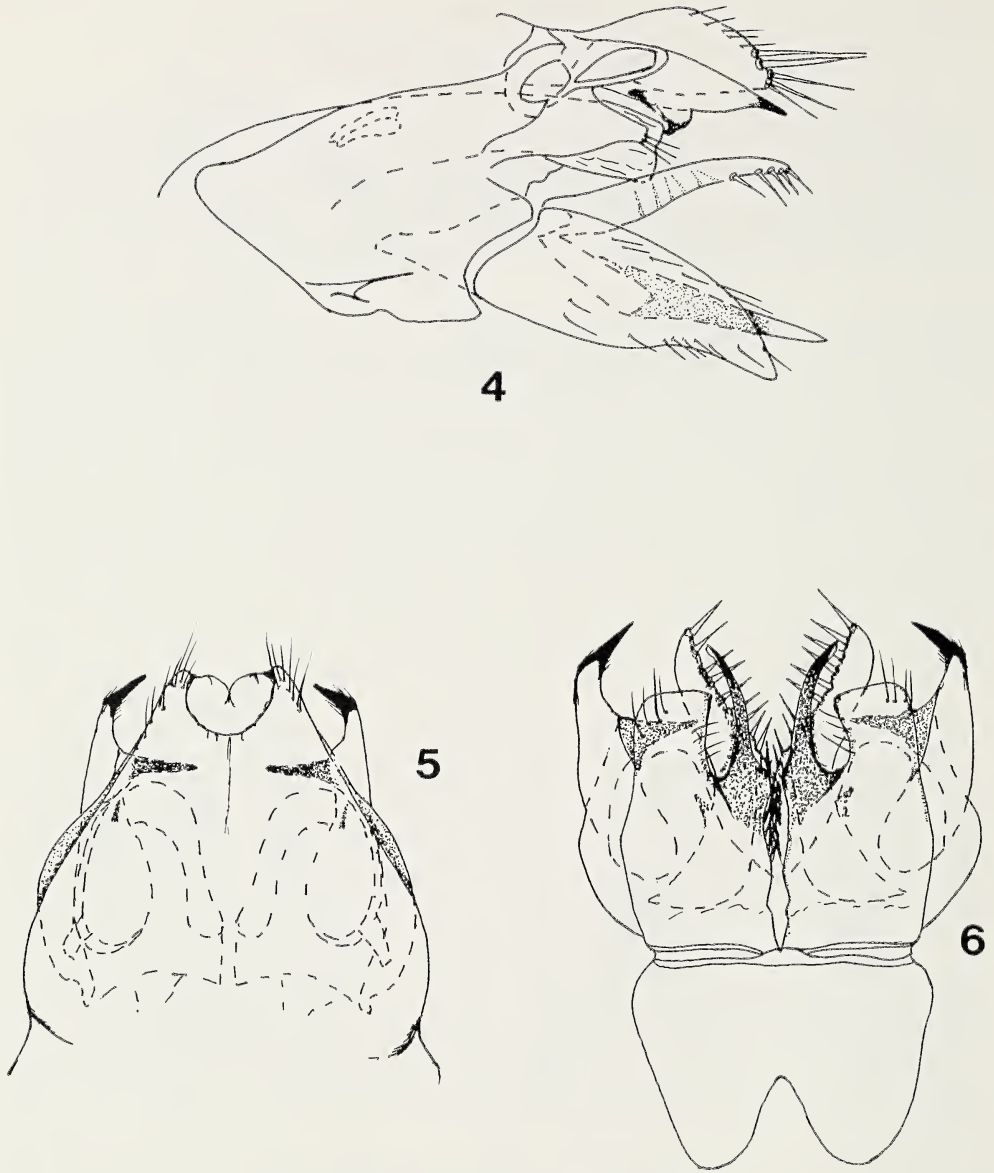


Fig. 4-6.—*Cernotina nigridentata*, new species, male genitalia; 4, lateral view; 5, dorsal view; 6, ventral view.

lobe flanked laterally by lightly sclerotized posterolateral extension of dorsum; lateral aspect halfmoon-shaped with blunt posterior margin bearing long setae. Preanal appendages with dorsolateral lobe elongated, gradually tapering to a single finger-shaped, blackened posterodorsal apex, center of ventromesal margin expanded into broad, black, pointed process directed ventromesad; ventromesal lobe produced posteriorly with several setae on truncate apex. Inferior appendages long, in lateral view with rounded apex curved slightly ventrad, ventral aspect of the main body with truncate and broad apex; anterodorsal lobe almost as long as main body, slightly sinuous with a row of large setae mesally; posteromesal lobe bladelike, elongated, well separated from the main lobe, longer than main body of

inferior appendages and gradually tapering to sharp apex curved laterad. Phallus tubular with two internal spines and several membranous folds at the apex.

Remarks.—This species is closely related to *C. harrisi*. It differs most noticeably in the shape of the inferior appendages with a distinct posteromesal lobe which is well defined and longer than the main body, and segment X which is broad and not divided into two distinct lobes.

Type Specimens.—Holotype, male, Peru: Departamento Loreto, banks of Yanomono Creek just below Explorama Lodge, 10 January 1993, J. L. Davenport. Paratype, same data as holotype, one male.

Etymology.—Latin for black-toothed, referring to the dark processes on the preanal appendages.

Cernotina aestheticella, **new species**
(Fig. 7–9)

Diagnosis.—This species may be recognized by a combination of characters including the divided ventromesal lobe and bifid dorsolateral lobe of the preanal appendages, fused anterodorsal aspect of segment X, and short, free apical section of the anterodorsal lobe of inferior appendages.

Description.—Male: length 3.5 mm. Legs and antennae yellowish, rest of body yellowish brown, wings pale brown. Wing venation and general structure typical for genus. Lateral view of ninth abdominal segment triangular with rounded anterior and posteroventral section, ventral aspect broad, anterior margin with round, deep incision, lateral margins indented in middle. Dorsal aspect of segment X membranous, partially divided with narrow groove along midline and shallow, triangular incision in apical margin; lateral aspect sinuate, curved ventrad with anteroventral margin covered by leaf-like, pointed scales and with elongated apices slightly directed dorsad. Preanal appendages fused ventrolaterally with segment X, dorsolateral lobe bifid with apex produced into beak-shaped structure with two long, black spines, ventromesal lobe divided into two sections; main ventromesal body with elongated, slender posterior section and narrow anterolateral process covered by small dents with shallow incision at apex. Inferior appendages with anterodorsal lobe partially fused with and shorter than main body of inferior appendages and produced into club-shaped, free apical section; posteromesal lobe not separated from main body and forming darkened, hook-shaped, short process. Phallus membranous, indistinct internally with two dark spines.

Remarks.—This species is related to *C. declinata* Flint from which it differs by the shape and structure of the preanal appendages, the rounded apex of the inferior appendages, and segment X with a triangular incision in the apical margin. The most unusual characteristic which clearly separates this species from any known *Cernotina* is the additional lateral process from the ventromesal lobe of the preanal appendages. Additional material of this species is needed to determine the morphology and taxonomical significance of this character.

Type Specimen.—Holotype, male, Peru: Departamento Loreto, bank of Yanomono Creek just below Explorama Lodge, 10 January 1993, L. J. Davenport.

Etymology.—Named for its aesthetically pleasing morphological structures.

Cernotina ecotura, **new species**
(Fig. 10–14)

Diagnosis.—This species is characterized by specific morphological features found in male genitalia that include the dorsolateral lobe of the preanal appendages with broad base tapering to a long, slender apical section with pointed apex directed dorsomesad, cup-shaped main body of the inferior appendages with fused and complex posteromesal lobe and miniature anterodorsal lobe.

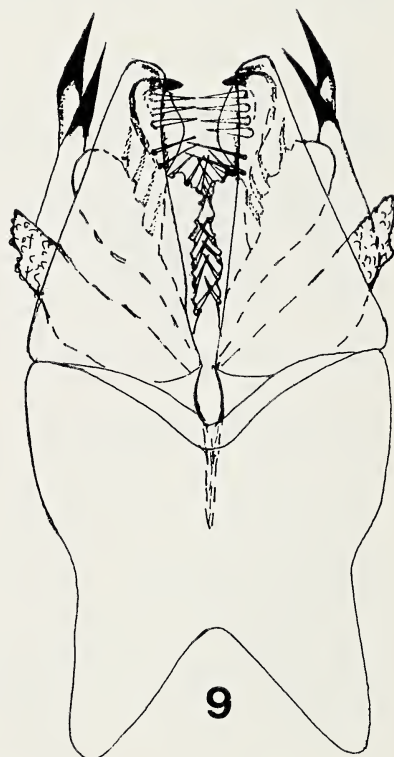
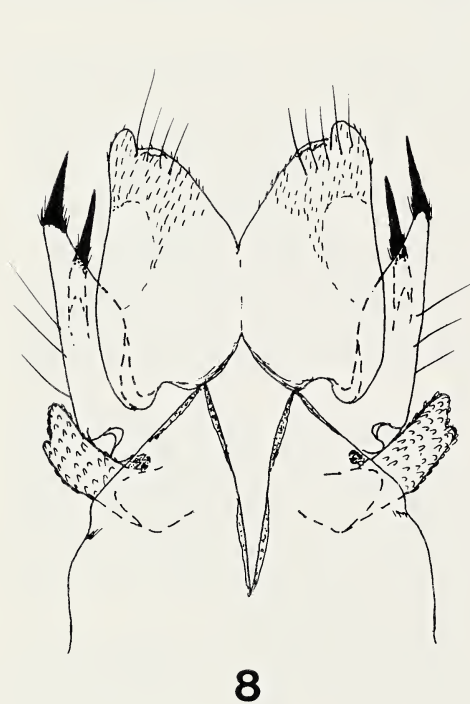
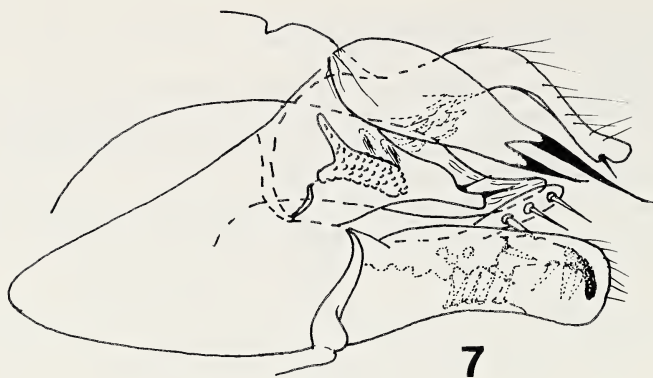


Fig. 7-9.—*Cernotina aestheticella*, new species, male genitalia; 7, lateral view; 8, dorsal view; 9, ventral view.

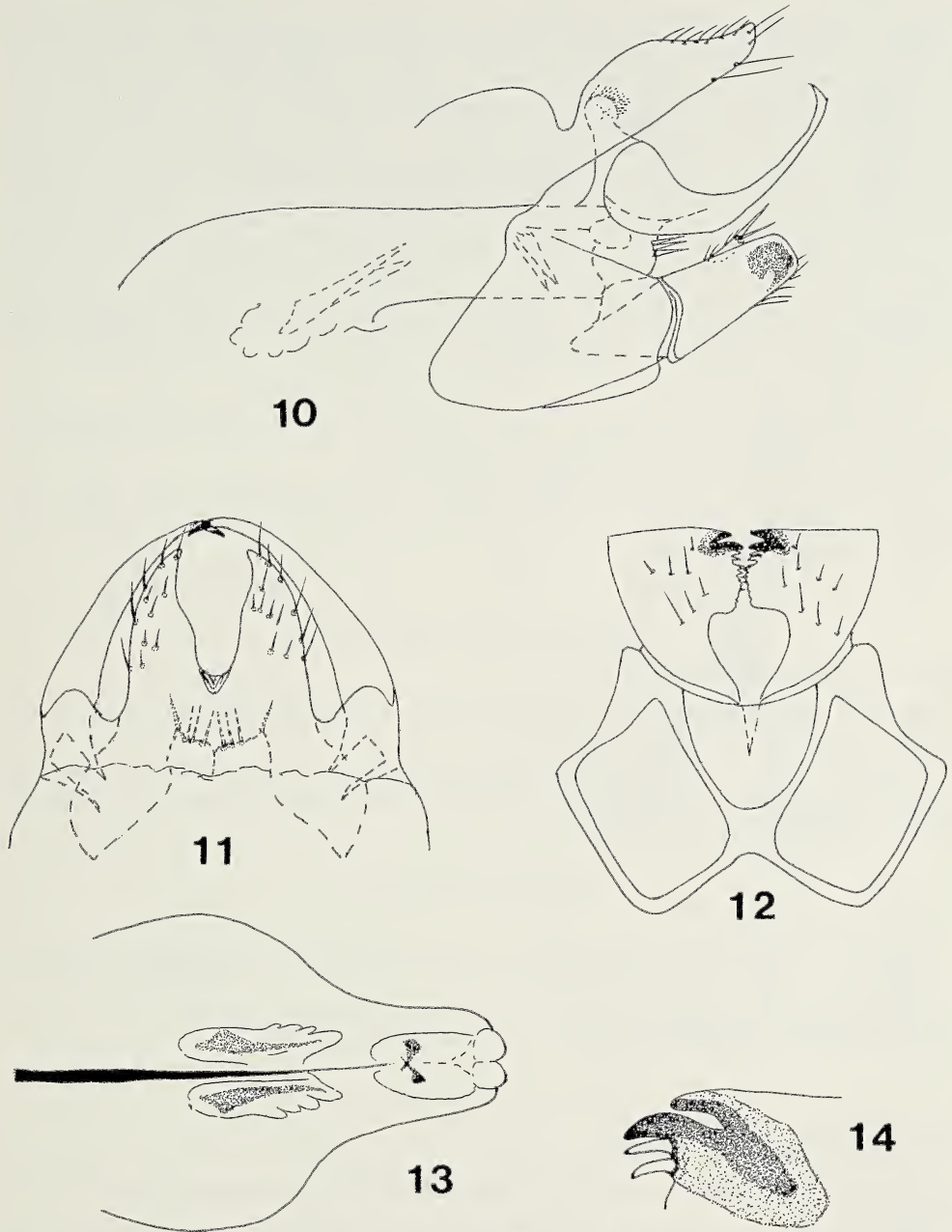


Fig. 10–14.—*Cernotina ecotura*, new species, male genitalia; 10, lateral view; 11, dorsal view; 12, ventral view; 13, phallus, dorsal view; 14, posteromesal lobe of inferior appendages, ventral view.

Description.—Male: length 4.0 mm. Body, legs, and antennae yellowish brown in alcohol, wings colorless and transparent. Wing venation and general structure typical for genus. Ninth segment in lateral view almost triangular with rounded posterior and anteroventral margins; ventral aspect broad with exoskeleton forming “sunglass frame” structure. Segment X lightly sclerotized, deeply incised middorsally forming broad lateral lobes with pointed apices sparsely covered with long setae and directed posteromesad, in lateral view roughly triangular with rounded anterodorsal portion and straight ventral margin. Preanal appendages bilobed; dorsolateral lobe with rounded anterodorsal margin and broad base tapering to long, narrow apical portion slightly bent dorsad with pointed apex directed dorsomesad; ventromesal lobe short, broad, and truncate with eight setae on posterior margin and two tubercles on posterolateral corners. Inferior appendages with rudimentary, short, and verrucous anterodorsal lobe with several small setae on dorsal and posterior margins; posteromesal lobe fused with main lobe forming complex dark structure with posteromesal corners bearing two black, hook-shaped teeth and two lightly colored spines; main body of inferior appendages in lateral view almost quadrangular with rounded apex, ventral aspect cup-shaped with verrucous mesal margin. Phallus extended into relatively short, tubular apical section and broad posterior portion; pair of large straight spines posteriorly and two slightly curved, shorter spines apically.

Remarks.—This species is unique and does not seem to be related to any of the known species of *Cernotina*. The structure of the preanal and inferior appendages is unlike any other species of *Cernotina*.

Type Specimen.—Holotype, male, Brazil: Estado Roraima, Boa Vista, Río Branco, December 14, 1995, Dr. Jan Wilt and George Hendrych. Paratype, same data as holotype, one male.

Entomology.—Named for Ecotur Park, the base camp of the expedition.

Cernotina bibranchiata Flint

Cernotina bibranchiata Flint, 1971:37.

Record.—This species was reported from the Amazon basin in Brazil (Flint, 1971). This is a new record for Peru.

Material.—Peru: Departamento Loreto, blackwater creek outlet of Lake Shimigay 2 km upstream of Napo River from mouth of Sucusari River, 15 January 1993, L. J. Davenport, one male.

Cernotina cygnea Flint

Cernotina cygnea Flint, 1971:37.

Record.—Flint (1971) described this species from the Amazon River basin in Brazil. It is a new record for Peru.

Material.—Peru: Departamento Loreto, edge of quiet backwater adjoining Explornapo Camp, 15 January 1993, L. J. Davenport, one male.

Cernotina decembens Flint

Cernotina decembens Flint, 1971:37.

Cernotina decumbens Flint, 1971:62.

Report.—Flint (1971) reported this species from the Amazon River basin in Brazil.

Material.—Brazil: Estado Roraima, Río Aqua Boa, December 15, 1995, Dr. Jan Wilt and George Hendrych, one male.

Cernotina spinigera Flint (Fig. 15–19)

Cernotina spinigera Flint, 1971:38.

Record.—This species is widely distributed in the Amazon River basin. In order

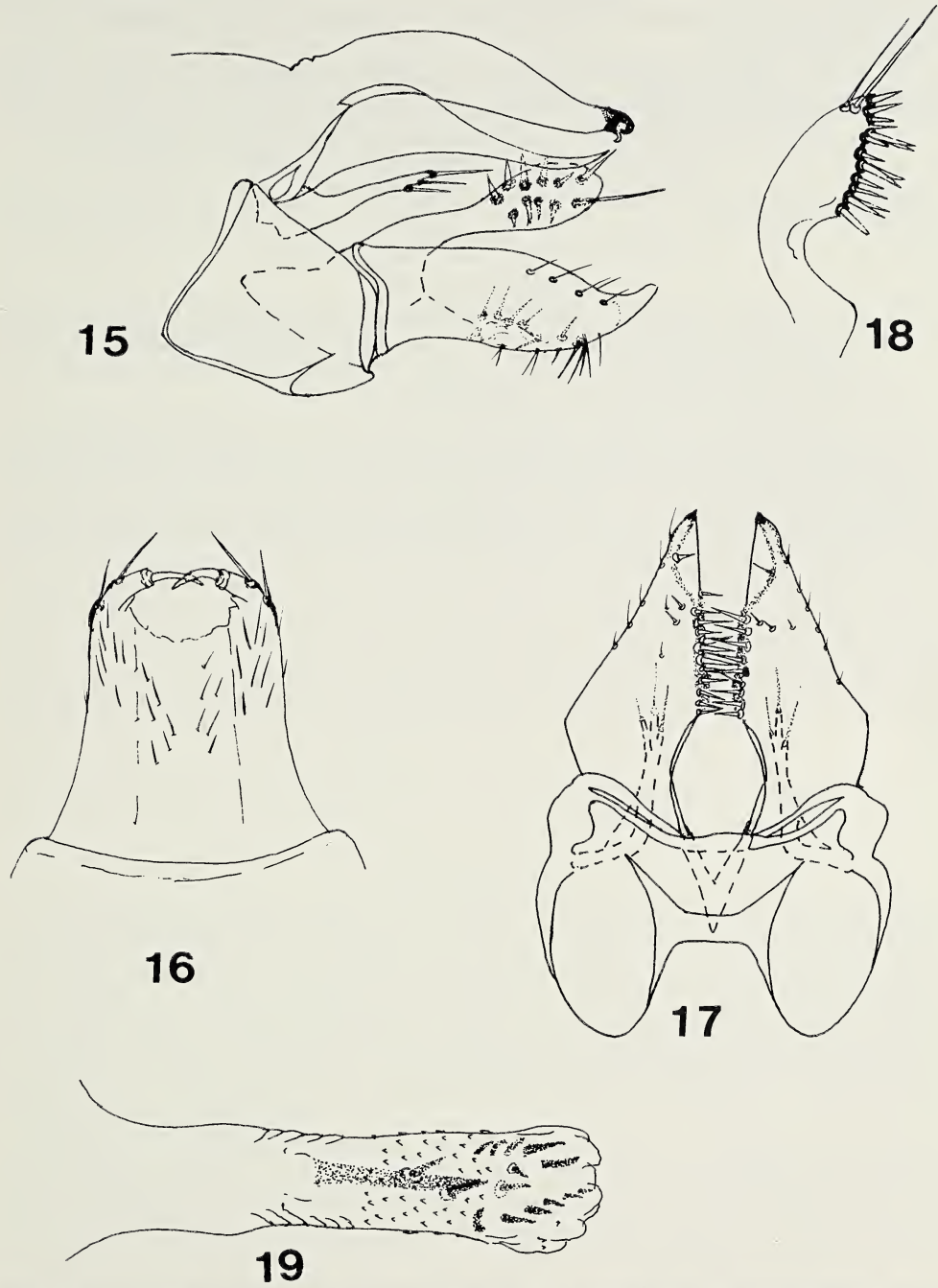


Fig. 15–19.—*Cernotina spinigera* Flint, male genitalia; 15, lateral view; 16, tenth segment, dorsal view; 17, ventral view; 18, anterodorsal lobe of inferior appendages, dorsal view; 19, phallus, dorsal view.

to facilitate identification of this species, new figures of male genitalia are included in this paper.

Material.—Brazil: Estado Roraima, Boa Vista, December 15, 1995, George Hendrych and Dr. Jan Wilt, one male.

ACKNOWLEDGMENTS

The help of Dr. Oliver S. Flint, who compared the specimen of *C. spinigera* Flint with the paratype, is gratefully appreciated.

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ATOKAN (LATE BASHKIRIAN OR EARLY MOSCOVIAN) BRACHIOPODS
FROM THE HARE FIORD FORMATION OF ELLESMERE ISLAND,
CANADIAN ARCTIC ARCHIPELAGO

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ABSTRACT

The Atokan (late Bashkirian or early Moscovian) brachiopod fauna from the lowermost Hare Fiord Formation in northern Ellesmere Island consists of at least 62 species, of which 18 are new, in at least 53 genera, of which three are new. New genera are the productoid *Lazarevia*, type species *L. stepanowensis* n. sp., the stenoscismatoid *Careoseptum*, type species *C. septentrionalis* n. sp., and an externally similar rhynchonelloid, *Exlaminella*, type species *E. insolita* n. sp. Other new species include *Orthotichia dorsistrigis*, *Plicatiferina kalashnikovi*, *Rugivestis pristina*, *Maemia gelida*, ?*Fimbrinia borealis*, *Liraria paucispina*, ?*Elassonia sverdrupensis*, *Antronaria annosa*, *Camarium nuperum*, *Nucleospira aquilonaris*, *Tiramnia walteri*, *Tiramnia grunti*, ?*Heteraria canadiensis*, *Elinoria ellesmerensis*, *Parachoristites tellevakensis*, and *Cranaena nassichuki*. This diverse fauna bears clear northern European Russian affinities, as do similar-age faunas from the northern Yukon Territory and south-eastern Alaska. This suggests that there was an open seaway which allowed free faunal dispersion and communication between northern European Russia to the east and also with the northern Yukon Territory and the southeastern Alaska Alexander Terrane to the southwest.

KEY WORDS: brachiopods, Carboniferous, Arctic, Ellesmere Island, Hare Fiord Formation

INTRODUCTION

The brachiopod fauna that is the subject of this paper was recovered from fenestellid bryozoan reefs at the base of the Hare Fiord Formation on both the north and south sides of Hare Fiord, northern Ellesmere Island. Although Carter (in Nassichuk, 1975) identified Carboniferous brachiopods from the Otto Fiord Formation from directly beneath the Hare Fiord Formation, the present paper constitutes the first description of Carboniferous brachiopods from Ellesmere Island and the first description of Upper Carboniferous brachiopods from the Canadian Arctic Archipelago.

The Hare Fiord Formation was named by Thorsteinsson (1970) for a succession of limestone, siltstone, and shale up to 732 m (2400 ft) thick within the Sverdrup Basin. This basin was formed by rifting of the Precambrian and Lower Paleozoic rocks of the Franklinian Geosyncline and contains approximately 14 km of upper Paleozoic through Cenozoic siliciclastic, carbonate, and evaporitic sediment. The Sverdrup Basin sequence rests unconformably on lower Paleozoic basement rocks of the Franklinian Geosyncline. The Hare Fiord Formation was deposited near

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the center of the basin along its northeast–southwest axis that passes through northern Ellesmere Island. It is overlain by black shale, siltstone, and bedded chert of the Permian Van Hauen Formation and underlain by medium-bedded anhydrite, limestone, and shale of the Bashkirian Otto Fiord Formation.

In much of its outcrop region the Hare Fiord Formation consists of two distinctive parts, a lower biogenic limestone that ranges in thickness from a few tens of meters up to 345 m and an upper unit of limestone, siltstone, and shale. The lower reefoid part was informally designated the “Tellevak Limestone” in the Blue Mountains area south of Hare Fiord by Bonham-Carter (1966). Although the brachiopod fauna within this lower biohermal unit is rich and diverse, brachiopods are rare above it and appear to be of limited biostratigraphic value.

Carboniferous brachiopods in the vicinity of or north of the Arctic Circle in North America are poorly known. Waterhouse, in Bamber and Waterhouse (1971), listed and illustrated Carboniferous and Permian brachiopod faunas from the northern Yukon Territory. Gorveatt and Nelson (1975) later described several Carboniferous and Permian spiriferids from this same region. Waterhouse and Waddington (1982) described both Carboniferous and Permian spiriferellid brachiopods from the Yukon Territory and the Canadian Arctic Archipelago. Carter (1975*a*) described two small faunules believed to be of late Early Carboniferous age from Melville and Axel Heiberg islands. Carter (1975*b*) listed but did not illustrate brachiopods from the Otto Fiord Formation of Melville and Ellesmere islands. Bowsher and Dutro (1957) and Dutro (1987) listed Carboniferous brachiopods from the Lisburne Group of northern Alaska but did not illustrate them.

Because there are many genera in the lower Hare Fiord Formation that range into the Permian and because one of the described Permian faunas was originally ascribed to the Carboniferous, citations of published reports dealing with Permian brachiopod faunas follow. These include Høltedahl (1917), Axel Heiberg Island; Chernyshev and Stepanov (1916), Ellesmere Island (originally described as Carboniferous); Harker and Thorsteinsson (1960), Devon Island; Stehli and Grant (1971), Axel Heiberg Island; and Waterhouse and Waddington (1982), various Arctic islands. All of these described Permian faunas are relatively small with moderate diversity.

Faunal Composition

Late Paleozoic carbonate buildups commonly bear diverse invertebrate faunas, especially rich in lophophorates, and this is true for the “Tellevak Limestone” in the Blue Mountains and other smaller bioherms elsewhere in the lower part of the Hare Fiord Formation. Several of the collections studied here were made from the flanks of bryozoan mounds or “reefs” as described in Davies et al. (1989) and Nassichuk and Davies (1992). From essentially three rich collections we have discriminated over 60 species of articulate brachiopods, many of which are represented by very few specimens making certain identification difficult or impossible. The bulk of the species occur in a single collection from which Nassichuk (1975) described 15 species of Atokan ammonoids (GSC locality 56430). The level of brachiopod diversity in this collection approaches that in many of the individual collections seen in Cooper and Grant’s (1972–1976) monumental monograph on the rich pre-Tethyan Permian silicified faunas of west Texas, which was based on massive samples. Sampling efficiency is usually vastly greater for large silicified samples than for most “crackout” collections.

Table 1.—Summary table showing the taxonomic composition of the brachiopod fauna of the lower Hare Fiord Formation.

Group	Families	Genera	Species
Orthids	2	2	3
Orthotetids	1	1	1
Chonetids	2	2	2
Productids	8	20	21
Rhynchonellids	5	7	7
Pentamerids	2	2	2
Athyridids	2	2	2
Spiriferids	8	15	19
Retziids	1	1	1
Terebratulids	2	2	4

Because the genus is the basic taxonomic unit used in comparing brachiopods from widely separated basins or continents, only generic diversity of the Hare Fiord brachiopods is discussed below. Productids, rhynchonellids, and spiriferids make up the bulk of this fauna, as can be seen in Table 1, with several notable omissions or poor representations. For example, we found no inarticulates, few chonetids, only scraps of orthotetids, and but two unusual athyridid species.

For some of these genera the level of confidence in the generic-level identification is low because of the lack of interiors. This should be borne in mind when assessing Tables 1 and 2. Even if several of the identifications are incorrect, there is clearly an impressive number of both older and younger anachronisms in this biohermal fauna.

Orthids.—Two orthid genera, *Rhipidomella* and *Orthotichia*, are found in the lower part of the Hare Fiord Formation. The former, a very long-ranging genus, is not recognizable to the species level and cannot be compared with other North American species. The genus *Orthotichia* is represented in the lower Hare Fiord Formation by two species, including a new one, *O. dorsistrigis*. This genus is confined to Upper Carboniferous and Permian strata, first appearing in the late Bashkirian or early Moscovian. Only three species are known from the North American Upper Carboniferous: *O. schuchertensis* Girty, from the Belden Shale of Colorado and probably of Morrowan (Bashkirian) age according to Langen-

Table 2.—Ranges of lower Hare Fiord Formation anachronistic brachiopod genera. Possible misidentifications are marked with a (?).

Genus	Prior range	New range
Camarium	Silurian–Tournaisian	Silurian–Lower Moscovian
Retimarginifera (?)	Sakmarian–Kungurian	Lower Moscovian–Kungurian
Maemia	Late Moscovian	Lower Bashkirian–Upper Moscovian
Eomarginifera	Viséan	Viséan–Lower Moscovian
Eomarginiferina	Viséan	Viséan–Lower Moscovian
Fimbrinia (?)	Kasimovian	Lower Moscovian–Kasimovian
Pustula	Tournaisian–Serpukhovian	Tournaisian–Lower Moscovian
Liraria	Kungurian	Lower Moscovian–Kungurian
Fluctuaria	Viséan–Serpukhovian	Viséan–Lower Moscovian
Cenorhynchia	Asselian–Kazanian	Lower Moscovian–Kazanian
Hemileurus (?)	Asselian	Lower Moscovian–Asselian
Antronaria	Sakmarian–Artinskian	Lower Moscovian–Artinskian

heim (1991); *O. morganiana* Derby, from Desmoinesian beds in Nevada as reported by Langenheim (1991); and *O. nawtawaketensis* Watkins, 1974, from the Baird Formation of California and of Bashkirian or Moscovian age. Several Russian species have been described from the Bashkirian through lower Permian and their morphology and distribution are summarized by Lazarev (1976).

Orthotetids.—This group, common in the upper Carboniferous (Pennsylvanian) of the midcontinental portion of North America, is represented in the lower Hare Fiord fauna only by unidentifiable fragments.

Chonetids.—This is another poorly represented group in the lower Hare Fiord fauna. Only two genera were identified, *Chonetinella* and *Sokolskya*. The former ranges from Bashkirian to Kungurian and the latter ranges from Bashkirian to Kasimovian. In most of North America the two most common Atokan and Desmoinesian chonetoid genera are *Mesolobus* and *Neochonetes*, both of which are missing from Ellesmere Island collections.

Productids.—The productids are the most diverse group in this fauna with 21 species in 20 genera. They, along with the spiriferids and rhynchonelloids, make up the bulk of the Hare Fiord brachiopod fauna. The most common productids in the North American midcontinent are cosmopolitan genera such as *Antiquatonia*, *Linoproductus*, *Cancrinella*, *Kozlowskia*, and *Echinaria*, all represented in the Hare Fiord fauna.

The suborder Strophalosiidina is represented by only one genus, *Plicatiferina*. This genus also occurs in the Upper Bashkirian to Lower Moscovian of southeastern Alaska. In Russia, it ranges from the upper Moscovian into the Lower Permian.

Within the superfamily Productoidea the family Productellidae includes in the lower Hare Fiord the genera *Rugivestis*, *Krotovia*, *Lazarevia*, *Maemia*, and possibly *Eomarginiferina*, *Fimbrinia*, *Hystriculina*, and *Retimarginifera*. *Rugivestis* was described from the Permian of Oregon and also is known from the lower Moscovian through Lower Permian of Russia and Lower Permian of China. The Hare Fiord species is also found in the late Bashkirian or early Moscovian Ladrones Limestone of southeastern Alaska. *Krotovia* is most commonly reported from Viséan through Bashkirian strata but is rarely reported up through the Lower Permian. *Lazarevia* is a new monotypic genus. *Maemia* is otherwise known only from the late Moscovian of Cape Chaika, northern Russia. Lacking interiors the identity of the specimens identified as *Eomarginiferina* is not certain. That genus is previously known only from the Upper Viséan of Ireland. *Fimbrinia* previously ranged from the late Kazimovian into the middle Permian. *Hystriculina* normally ranges from the Kazimovian through the Sakmarian. *Retimarginifera* is a Permian genus. The family Productidae includes the genera *Reticulatia*, *Eomarginifera*, *Kutorginella*, and possibly *Kozlowskia*. *Reticulatia* is a cosmopolitan genus ranging from the Bashkirian through the Lower Permian. *Eomarginifera* is a Viséan European genus. The genus *Kutorginella* was described from the Moscovian of the Russian platform but it is also known from several species in Russia and North America ranging in age from Sepukhovian through Kungurian. In western Europe *Antiquatonia* is known only from the Lower Carboniferous but has been reported from the Upper Carboniferous as well as the Lower Carboniferous of Kazakhstan. In North America this genus first appears in the latest Mississippian and ranges upward into the Lower Permian. *Kozlowskia* is another cosmopolitan genus ranging from the Bashkirian through the Lower Permian.

The superfamily Echinoconchoidea is represented by the genera *Pustula* and

Echinaria. *Pustula* is used here in the broad sense because no interiors are known for these Arctic specimens. True *Pustula* is probably restricted to the Lower Carboniferous but the name is applied here to pustulose nonrugose specimens with rounded outlines. Their actual affinities are unknown. *Echinaria* ranges throughout most of the Upper Carboniferous. Winkler Prins (1968) reported this genus from the lower Moscovian of northern Spain.

The superfamily Linoproductoidea is represented by three genera. *Liraria* was previously known only from the Kungurian of Texas. An undescribed species also occurs in the upper Bashkirian or lower Moscovian of southeastern Alaska. *Fluctuaria* was previously restricted to the Viséan and possibly Serpukhovian of Eurasia. Kos'ko et al. (1993) reported it from the middle Bashkirian of Wrangel Island, Winkler Prins (1968) reported it from the upper Moscovian of northern Spain, and Kalashnikov (1980) reported it from the late Upper Carboniferous of Novaya Zemlya. *Cancrinella* ranges throughout most of the Upper Carboniferous and Permian. Reports from the Bashkirian and Moscovian are less common than from the Kasimovian and above. These small, fragile shells never seem to occur in abundance but have a remarkably wide distribution.

Rhynchonellids.—There are seven genera of rhynchonelloids in this fauna including *Cenorhynchia*, ?*Elassonia*, ?*Phrenophoria*, ?*Hemileurus*, *Septacamera*, and *Antronaria* plus the new genus *Exlaminella*. All of these genera except the latter have Permian type species and only *Septacamera* occurs in the Carboniferous, where it ranges down into the Bashkirian. Rhynchonellids in the Upper Carboniferous of the midcontinent are not generically diverse, mostly belonging to the genera *Wellerella*, *Leiorhynchoidea*, and the punctate genus *Rhynchopora*, none of which occur in this fauna. The undescribed late Bashkirian or early Moscovian rhynchonelloids from southeastern Alaska are also generically diverse judging from exteriors.

Stenoscismatoids.—Stenoscismatoids are represented by two genera, *Stenoscisma* and a new genus, *Careoseptum*. The former is cosmopolitan and long ranging. The latter is unique to the Hare Fiord Formation.

Athyridids.—There are two unusual athyridoids in this fauna, *Camarium* and *Nucleospira*. Whereas one would expect to find the cosmopolitan genera *Composita* and *Cleiothyridina* in any late Paleozoic fauna, they are absent here. Instead, the superfamily is represented by the above-named rare genera. *Camarium*, heretofore unknown above the Tournaisian (see Campbell and Engel, 1963, and Carter, 1967), greatly extends its stratigraphic range. *Nucleospira* is rare above the Viséan. Only two species of this genus are described from above the Viséan, one from the basal Morrowan and one from the Permian of west Texas.

Spiriferids.—With 19 species in 14 or 15 genera the spiriferids are nearly as diverse as the productids. There are two species of the ambocoelioid genus *Crurithyris*, five martinioids in three or four genera, seven species of spiriferoids in seven genera, (including four choristitids in four genera), two species of paeckelmanelloids of the genus *Cantabriella*, two species of the brachythyridoid *Meristorygma*, and one reticularioid. The choristitids and martinioids indicate strong affinities with northern Russian faunas. Few of these spiriferid genera have a narrowly restricted stratigraphic distribution. Most of them range throughout the Upper Carboniferous and Lower Permian. However, the paeckelmanelloid genus *Cantabriella* is previously known only from the Bashkirian and Moscovian of northern Spain.

Crurithyris ranges throughout the entire Carboniferous and most of the Perm-

ian. The martinoid genera *Tiramnia*, *Heteraria*, and *Jilinmartinia* occur in this fauna. Specimens of *Tiramnia* occur abundantly in most of the collections. This genus was originally described from the Upper Carboniferous and Permian of Taimyr, Novaya Zemlya, Timan, Ural Mountains, and Greenland. Besides this new occurrence in the Canadian Arctic Archipelago, this genus occurs in rocks of the same age in southeastern Alaska. *Heteraria* was described from the Permian of west Texas. It also occurs in the lower Moscovian of southeastern Alaska. *Jilinmartinia* is based on a Late Carboniferous species from northern China and also occurs in the Kasimovian of Bashkiria. A single small martinoid specimen of unusual proportions probably represents a new genus and species.

The spiriferoids are the most diverse superfamily of this order and include the genus *Anthracospirifer* of the family Spiriferidae. The family Choristitidae includes *Elinoria* and *Brachythyrina* of the subfamily Angiospiriferinae, *Parachoristites* and *Trautscholdia* of the subfamily Choristitinae, and *Tangshanella* of the subfamily Tangshanellinae. The trigonotretids are represented only by the genus *Gypospirifer* of the subfamily Neospiriferinae.

Anthracospirifer is a widespread North American Carboniferous spiriferid ranging from the lower Viséan (Keokuk) through the Moscovian (Desmoinesian). This genus is rare in Russia and its presence in the Hare Fiord Formation indicates North American faunal affinities. *Elinoria* is found in the upper Moscovian, Late Carboniferous, and Lower Permian of European Russia and the Donets Basin. It also is present in the lower Moscovian of southeastern Alaska as well as the Hare Fiord Formation. These North American occurrences extend the range down to the early Moscovian. *Brachythyrina* is rare in North America being reported from the very late Mississippian of Wyoming and the Bashkirian or Moscovian (Ettraint Formation) of Yukon Territory. The genus ranges throughout most of the late Paleozoic of Eurasia. *Parachoristites* is characteristic of the Bashkirian of Russia but ranges up into the Lower Permian. This is the first report of the genus from North America. *Trautscholdia* ranges throughout the entire Upper Carboniferous of Russia. Again, this is the first report of this genus in North America. *Tangshanella* was first described from the Upper Carboniferous of northeastern China and has subsequently been reported from the Tournaisian of Australia and the Upper Carboniferous of northwestern China and Japan. The neospiriferid *Gypospirifer* ranges from the Bashkirian into the Lower Permian and appears to have cosmopolitan distribution.

Retziids.—The retzioid genus *Hustedia* ranges throughout the late Paleozoic and is cosmopolitan.

Terebratulids.—Terebratulids generally are of little use in late Paleozoic age determination, the genera usually being long ranging. *Beecheria* appears in the Tournaisian and ranges into the Lower Permian. *Cranaena* is rarely reported in the Upper Carboniferous. It has been reported from the Devonian to the Lower Permian, although many of these reports have not been confirmed with interior morphological details.

Biostratigraphy

The Atokan (late Bashkirian or early Moscovian) age assigned to this brachiopod fauna is based on direct and indirect ammonoid, conodont, and foraminifer evidence. Nassichuk (1975) described a large ammonoid fauna from a reef on the north side of Hare Fiord (GSC locality 56430) ascribing an Atokan (or early

Moscovian) age to it. Conodont data published by Bender (1980) supported the early Moscovian age. Nassichuk and Davies (1992) suggested that the Atokan included late Bashkirian as well as early Moscovian strata. Newly discovered conodonts from GSC locality 56430 are being studied by T. Nemirovskaya and N. Sobolev who also have ascribed a late Bashkirian to early Moscovian age to the Hare Fiord.

Diagnostic foraminifers have been recovered from the lower Hare Fiord Formation by Mamet (in Nassichuk, 1975) who suggested an early Moscovian age. Groves et al. (1994) also correlated the Atokan with the late Bashkirian and early Moscovian and recovered both late Bashkirian and early Moscovian fusulinaceans from the coeval Nansen Formation.

The brachiopods, including taxa formerly ascribed to Viséan through Lower Permian stratigraphic ranges, are of much less utility in age determination. The presence of numerous genera which also have been reported in early Moscovian beds in the European portion of Russia, however, generally supports this age determination.

Anachronisms

Table 2 lists the genera which previously had substantially different stratigraphic ranges. Note that there are 12 genera of possible anachronisms, six younger and six older. Misidentifications might reduce this number but it is clear that the Hare Fiord brachiopod fauna represents an unusual upper Bashkirian to lower Moscovian biohermal biofacies unknown elsewhere. These anachronisms originally led us to assign a lower Permian age to the fauna on the assumption that the youngest faunal elements gave some indication of the true age of the fauna. The overwhelming evidence from the ammonoids and microfossils of an upper Bashkirian to lower Moscovian age of the lower Hare Fiord Formation forced us to reexamine and revise our preliminary taxonomic and biostratigraphic determinations.

Correlations and Paleobiogeography

Although the lower Hare Fiord Formation fauna described herein cannot be correlated directly with previously described brachiopod faunas of similar age from North America, it bears many similarities with the undescribed allochthonous faunas from the Ladrones Limestone and Klawak Formation of southeastern Alaska, Alexander Terrane. These coeval formations bear rich brachiopod faunas containing a number of distinctive Hare Fiord brachiopod genera that do not occur elsewhere in Bashkirian or Moscovian strata in North America, with the possible exception of the Yukon Territory. These include *Plicatiferina*, *Rugivestis*, *Fluctuaria*, *Liraria*, *Elinoria*, *Tiramnia*, *Gypospirifer*, *Meristorygma*, *Brachythyridina*, and *Heteraria*.

These diverse assemblages certainly provide a strong biogeographic link to the Ellesmere Island fauna of approximately the same age and suggest that they were connected by an unrestricted, if indirect, seaway. The exact location of this seaway is speculative but could have passed through the present Yukon Territory or perhaps through northeastern Alaska, both of which are known to bear largely undescribed early Moscovian (Atokan) faunas (Bamber and Waterhouse, 1971; Dutton, 1987).

Correlation with the remainder of North America, however, is much more dif-

ficult. Considering the present fauna, only *Kozlowskia splendens* (Norwood and Pratten), *Chonetinella* cf. *C. jeffordsi* Stevens, *Reticulatia* cf. *R. americana* Dunbar and Condra, *Antiquatonia* cf. *A. hermosana* (Girty), and *Anthracospirifer* cf. *A. occiduus* Sadlick suggest a Pennsylvanian age, ranging from Atokan to Virgilian.

Several Moscovian species were illustrated or listed from the Upper Carboniferous of northern Yukon Territory by Bamber and Waterhouse (1971) and Gorveatt and Nelson (1975). Most of these species were later assigned a late Moscovian age by Waterhouse and Waddington (1982). Two small faunules designated as the "*Martiniopsis*" Zone and the *Buxtonia* Zone, however, were later assigned to the early Moscovian by Waterhouse and Waddington (1982). None of the species listed or illustrated show much similarity to those of the Ellesmere Island fauna but the presence of so-called *Choristites* and "*Martiniopsis*" in the Yukon collections suggest Russian affinities. In the late Moscovian faunas the presence of *Waagenoconcha* and abundant *Choristites* suggest the same affinities. The spiriferids described by Gorveatt and Nelson (1975) were dated as late Moscovian and also clearly indicate Russian affinities.

In summary, the faunas from limestone reefs in the lower part of the Hare Fiord Formation, from the Ettrain Formation of northern Yukon Territory, and from the Ladrones Limestone and Klawak Formation of southeastern Alaska all have strong affinities with those of northern European Russia and with each other. The faunas from the Alexander Terrane of southeastern Alaska may be allochthonous but the close similarity between those faunas and those from the lower Hare Fiord clearly suggest an open marine communication between the two regions.

Correlations with upper Bashkirian or lower Moscovian strata in northern European Russia is difficult, being dependent mainly on faunal lists. Kalashnikov (1980) reviewed late Paleozoic brachiopod faunas from this region and listed species for numerous localities and horizons in the general area encompassing Novaya Zemlya, Cape Chaika, Timan, and the northern Urals. However, most of his illustrations are of specimens from younger beds. The following genera from the lower Hare Fiord Formation are reported by Kalashnikov from Bashkirian or Lower Moscovian beds in northern Russia: *Rhipidomella*, *Eomarginifera*, *Rugivestis*, *Kozlowskia*, *Antiquatonia*, *Krotovia*, *Kutorginella*, *Reticulatia*, *Fimbrinia*, *Linoproductus*, *Fluctuaria*, *Septacamera*, *Parachoristites*, *Purdonella*, *Brachythyridina*, *Elinoria*, *Meristorygma*, *Phricodothyris*, *Cranaena*, and *Tiramnia* (Kalashnikov includes numerous references to various species of *Martinia*, some of which probably belong in *Tiramnia*). This assemblage is unique to northern Russia and Ellesmere Island but also includes many cognate genera in southeastern Alaska.

GSC LOCALITIES

Figure 1 shows Geological Survey of Canada (GSC) localities where late Bashkirian to early Moscovian brachiopods were found in the Hare Fiord Formation. Descriptions of these localities follow.

GSC Locality C-4083.—In the saddle of a northeast–southwest trending ridge about eight km northwest of Mount Barrell and immediately west of Wood Glacier (80°54'N, 84°11'W). The locality is in thin-bedded, dark grey limestone, about 46 m above the base of the Hare Fiord Formation. It is in the nonreef facies of

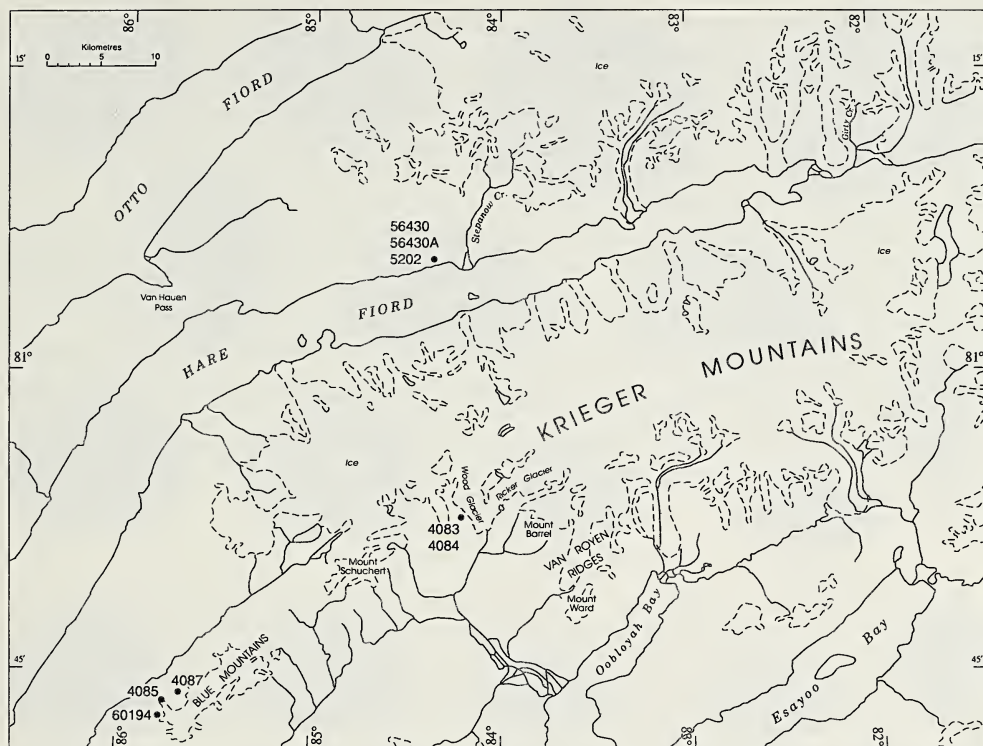


Fig. 1.—Index map showing Geological Survey of Canada (GSC) localities for the Upper Carboniferous brachiopods described in this report, from both the north and south sides of Hare Fiord, northern Ellesmere Island. Most of the fossils are from GSC locality 56430 in a small bryozoan bioherm on the north side of Hare Fiord. GSC locality 56430A is from the same stratigraphic level as GSC locality 56430 but is 3 m farther to the west. Similarly, GSC locality C-5202 is 1.5 m stratigraphically below locality 56430. GSC localities C-4083 and C-4084 are in thin argillaceous limestone some 45.72 m (150 ft) above the base of the Hare Fiord Formation west of Wood Glacier; GSC locality C-4084 is 60.96 m (200 ft) along strike to the west of GSC locality C-4083. GSC localities C-4087, C-4085, and 60194 in the southern Blue Mountains occur in the upper part of a bryozoan reef complex that Bonham-Carter (1966) informally named the “Tellevak Limestone” in the lower Hare Fiord Formation. Dashed lines indicate boundary of permanent ice.

the formation and was discovered originally by W. W. Nassichuk and C. Spinosa (Boise State University) in 1969.

GSC Locality C-4084.—This locality is in the same stratigraphic position 61 m along strike to the west of GSC locality C-4083. This locality is in the nonreef, basal facies of the Hare Fiord Formation.

GSC Locality C-4085.—This locality occurs in light grey skeletal limestone in the upper three m of the informally designated “Tellevak Limestone” in the Hare Fiord Formation. It is on the southwestern side of the Blue Mountains, 5.8 km northeast of the northern tip of Hare Fiord Diapir (80°44'N, 85°40'54"W). The locality is in a creek bottom near the terminus of the southernmost large westerly directed glacial tongue flowing from a small ice field in the southern Blue Mountains. This locality was discovered by W. W. Nassichuk and C. Spinosa (Boise State University) in 1969.

GSC Locality C-4087.—This locality is in the upper part of the “Tellevak

Limestone" in the lower Hare Fiord Formation on the northwest side of the Blue Mountains, 1.3 km east-northeast of GSC locality C-4085.

GSC Locality 56430.—Principal brachiopod locality. Near the top of a small bryozoan mound about 30 m above the base of the Hare Fiord Formation. This locality is less than 300 m north of the fiord and 3.2 km west of the midpoint of the delta formed by Stepanow Creek (81°07'30"N, 84°20'W). Collected by W. W. Nassichuk and various field associates in 1963, 1969, and 1971.

GSC Locality 56430A.—In the same stratigraphic position as GSC locality 56430 and within the same small bryozoan mound but three m farther to the west.

GSC Locality C-5202.—This is the same general location within the same bryozoan mound as GSC locality 56430, only 1.5 m stratigraphically lower.

GSC Locality 60194.—Upper part of the reefoid "Tellevak Limestone" in the lower Hare Fiord Formation. The locality is 174 m above the top of the underlying Otto Fiord Formation (Bashkirian) which contains mainly anhydrite, shale, and limestone. It is ten km east of eastern shore of Hare Fiord, southern Blue Mountains, northern Ellesmere Island (80°44'11"N, 85°45'40"W). Collected by G. F. Bonham-Carter (Geological Survey of Canada) in 1963.

SYSTEMATIC PALEONTOLOGY

In the following section we have used the relatively recent classifications of Brunton et al. (1995) for the productoids and Afanas'eva (1988) for the chonetoids. For the spiriferids we have used the revised classification of Carter et al. (1994). The rhynchonellid classification follows that of Savage (1996). For the other groups we have generally followed the classification in the original Treatise on Invertebrate Paleontology (Williams et al., 1965).

All types are deposited in the type collections of the Geological Survey of Canada, Ottawa. The remainder of the specimens are in the collections of the Institute of Sedimentary and Petroleum Geology, Calgary.

Phylum Brachiopoda Duméril, 1806

Class Articulata Huxley, 1869

Order Orthida Schuchert and Cooper, 1932

Suborder Orthidina Schuchert and Cooper, 1932

Superfamily Enteletoidea Waagen, 1884

Family Rhipidomellidae Schuchert, 1913

Genus *Rhipidomella* Oehlert, 1890

Rhipidomella sp.

(Fig. 2.1, 2.2)

Discussion.—There are two specimens of this genus in the collection from GSC locality 56430, plus one ventral valve from GSC locality 56430A. The large incomplete specimen is broad and thin bodied, similar in some respects to *Rhipidomella oweni* Hall and Clarke from the Lower Viséan of Kentucky or *Rhipi-*

Fig. 2.—Orthids. 2.1, 2.2, *Rhipidomella* sp., GSC 115535; dorsal and ventral views, $\times 1.5$. 2.3–2.7, *Orthotechia* sp., GSC 115536; ventral, dorsal, lateral, anterior, and posterior views, $\times 1$. 2.8–2.37, growth series of *Orthotechia dorsistrigis* n. sp., including the holotype (Fig. 2.8–2.12, GSC 115537) and five paratypes, GSC 115538–115542, respectively, $\times 1$.



Table 3.—*Measurements (in millimeters) of the types of Orthotichia dorsistrigis n. sp.*

GSC number	Locality	Length	Width	Thickness
115537	56430	19.5	24.1	13.0
115538	56430	17.2	21.2	11.4
115539	56430	16.9	19.0	10.4
115540	56430A	13.6	19.5	8.7
115541	56430	13.7	16.7	8.0
115542	56430	11.4	12.6	7.8

domella pressula Lazarev from the Moscovian of the polar Urals. The other specimens are much smaller but of similar proportions.

Family Enteletidae Waagen, 1884
 Subfamily Schizophoriinae Schuchert, 1929
 Genus *Orthotichia* Hall and Clarke, 1892
Orthotichia dorsistrigis, **new species**
 (Fig. 2.8–2.37)

Holotype.—GSC 115537, Figures 2.8–2.12, from GSC locality 56430.

Paratypes.—GSC 115538, 115539, 115541, and 115542, Figures 2.13–2.22, 2.28–2.37, from GSC locality 56430; GSC 115540, Figures 2.23–2.27, from GSC locality 56430A.

Description.—Medium size, unequally biconvex; outline transversely subovate; dorsal valve equal to or slightly longer than ventral valve; maximum width attained slightly anterior to midlength; hinge-line about equal to half of maximum width; anterior margin slightly emarginate and weakly uniplicate; ventral sulcus weakly developed; dorsum with distinct secondary sulcus on fold in anterior half or two-thirds of valve; lateral profile moderately thin, guttate; cardinal extremities of both valves slightly compressed; entire surfaces of valve regularly capillate.

Ventral valve slightly thinner than opposite valve, moderately to weakly convex with slightly inflated umbonal region; sulcus broad, shallow, confined to anterior half of valve, with low median fold in rare specimens; beak small, overhanging nearly catacline low, widely triangular interarea; delthyrium about as wide as high; ventral interior with long, high dental plates and low, thick median ridge; other details unknown.

Dorsal valve slightly to moderately thicker than ventral valve, most convex in umbonal region, flanks sloping evenly to lateral margins; umbonal region slightly inflated and projecting posterior to hingeline with small incurved beak; dorsum broadly depressed in most mature specimens forming shallow sulcus; dorsal interarea low, orthocline; dorsal interior with moderately thickened cardinal process and long, high, diverging brachiophore plates; other details unknown.

Measurements of Types.—See Table 3.

Diagnosis.—This species is characterized by its moderate size, transverse outline, thin profile, shallow broad ventral sulcus, and dorsal sulcus.

Comments.—*Orthotichia pentagona* (Eichwald, 1860), from the Bashkirian of Ukraine and Russia, is much larger than *O. dorsistrigis* n. sp. with a subpentagonal outline and stronger dorsal sulcus and ventral fold. A dorsal sulcus is also found in the specimen described as *Orthotichia?* sp. by Yanagida (1975), from the upper Moscovian of Thailand.

Distribution.—GSC locality 56430 (36 specimens); GSC locality C-5202 (five specimens).

Orthotichia sp.
 (Fig. 2.3–2.7)

Comments.—There are two large orthotichias from GSC locality 60194 that are clearly distinct from the new species described above as *O. dorsosulcata* n.

sp. These large specimens lack the dorsal sulcus seen in that species. They appear to be similar to *Orthotichia schuchertensis* Girty, 1903, from the Hermosa Formation of Colorado, in having discontinuous and disproportionately deep inter-spaces defining some of the irregularly strong costellae.

Distribution.—GSC locality 60941 (two specimens).

Order Strophomenida Öpik, 1934
Suborder Orthotetidina Waagen, 1884
Unidentifiable orthotetoid

Comments.—There are seven fragmentary specimens of orthotetids in the Hare Fiord collections. They seem to belong to an unusually thin, flattened form of unknown generic affinities. The largest fragment, which is approximately 53 mm wide by 36 mm long, is apparently a flattened dorsal valve. There is no indication of plates in either valve of these fragments and preservation is imperfect.

Distribution.—All seven specimens are from GSC locality 56430.

Suborder Chonetidina Muir-Wood, 1955
Superfamily Chonetoidea Bronn, 1862
Family Rugosochonetidae Muir-Wood, 1962
Subfamily Rugosochonetinae Muir-Wood, 1962
Genus *Chonetinella* Ramsbottom, 1952
Chonetinella cf. *C. jeffordsi* Stevens, 1962
(Fig. 3.6)

*1962 *Chonetinella jeffordsi* Stevens, p. 627, pl. 93, fig. 18, 19.

Description.—Medium size; moderately thick; ventral umbo moderately inflated and extending well posterior to hingeline; cardinal extremities defined by concave flexures; venter moderately broad with narrow, shallow, rounded sulcus that originates near beak; ornament of about 20 to 21 capillae per five mm near anterior margin; dorsal valve and interiors unknown.

Comments.—This single specimen is similar to specimens of *Chonetinella jeffordsi* Stevens, 1962, described and illustrated by both Stevens and Sutherland and Harlow (1973:34).

Distribution.—GSC locality 56430 (one specimen).

Subfamily Chalimochonetinae Afanas'eva, 1988
Genus *Sokolskya* Aizenverg, 1980
? *Sokolskya* sp.
(Fig. 3.5)

Description.—A single large chonetid ventral valve is tentatively assigned here to the genus *Sokolskya* Aizenverg on the basis of its large size, weakly convex profile with flattened umbonal region, fine ribbing, and short thin ventral septum.

Distribution.—GSC locality 56430 (one specimen).

Suborder Strophalosiidina Waagen, 1883
Superfamily Strophalosioidea Schuchert, 1913
Family Araksalosiidae Lazarev, 1989
Subfamily Quadratiinae Lazarev, 1989
Genus *Plicatiferina* Kalashnikov, 1980
Plicatiferina kalashnikovi, new species
(Fig. 3.1–3.4)

Holotype.—An incomplete ventral valve showing the hingeline spines, GSC 115544, from GSC locality C-5202, Figure 3.2.

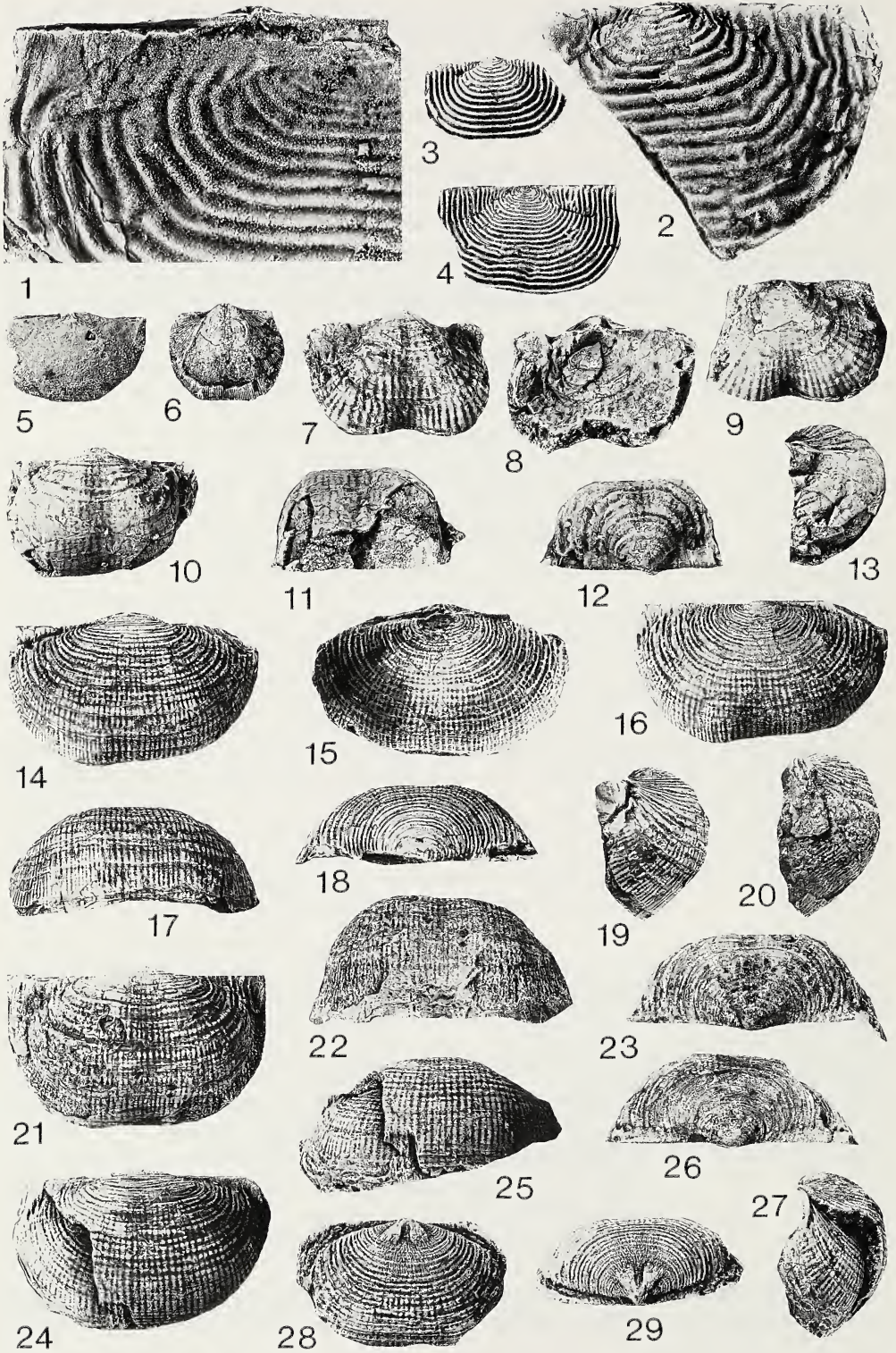


Table 4.—Measurements (in millimeters) of the types of *Plicatiferina kalshnikovi* n. sp.

GSC number	Locality	Length	Width
115543	56430A	15.0+	18.6+
115544	C-5202	19.1+	24.3+
115545	56430A	14.1	21.3+
115546	C-5202	16.6	25.7

Paratypes.—A ventral valve with a disarticulated dorsal valve impressed against it, GSC 115543, from GSC locality 56430A, Figure 3.1; a small ventral valve, GSC 115545, from GSC locality 56430A, Figure 3.3; a natural mold of a dorsal valve exterior, GSC 115546, from GSC locality C-5202, Figure 3.4.

Description.—Medium size; outline transversely subquadrate; maximum width at hingeline; very thin profile; both valves flattened, nearly planoconvex with very thin body cavity; both valves entirely covered with slightly irregular concentric rugae, numbering about nine to 12 per cm in largest specimens.

Ventral valve weakly convex with weakly concave lateral extremities; beak very small, projecting slightly posterior to hingeline; umbonal region very slightly inflated, remainder of valve flattened; interarea flattened or slightly concave, low, apsacline; delthyrium apparently open; five or more pairs of regularly spaced spines at hingeline directed posterolaterally at angle of 30 to 45 degrees to hingeline; fine low spines on body of shell rare, scattered, on small nodes or occasionally short, elongate ridges; teeth small; other interior details unknown.

Dorsal valve nearly flat; dorsal interarea absent or not observed; spines absent; rugae as in opposite valve; interior with low bilobed cardinal process; other internal details not observed. (Note: a dorsal interior from the Ladrone Limestone of southeastern Alaska has an alveolus in front of a small bilobed cardinal process which is flanked by small transverse tooth sockets. The specimen is spalled anteriorly and no muscle scars or other internal details are indicated.)

Diagnosis.—Medium size *Plicatiferina* with nearly regular concentric rugae and a row of hingeline spines directed posterolaterally at a moderately low angle to the hingeline.

Measurements.—See Table 4.

Comparisons.—This species externally resembles the holotype of *Plicatiferina pseudoplicatilis* (Stepanov, 1948), from the Carboniferous (Moscovian or Kasi-movian?) of Bashkiria, differing mainly in its more regular rugae. A row of hingeline spines has never been reported in this species. Stepanov's paratypes have a more rounded outline with irregular bifurcating rugae than this Hare Fiord species. Kalashnikov (1980) and Lazarev (1990:pl. 40, fig. 8–11) illustrated specimens of *P. neoplicatilis* (Stepanov, 1939) from Cape Chaika showing this irregular rugation, as does *P. borealica* Kalshnikov, 1980. All of these Russian species

←

Fig. 3.—Chonetoids, strophalosioids, and productoids. 3.1–3.4, *Plicatiferina kalshnikovi* n. sp.; 3.1, dorsal view showing ventral interarea and teeth, GSC 115543, $\times 4$; 3.2, the holotype, a ventral valve showing spine bases at hingeline, GSC 115544, $\times 2$; 3.3, 3.4, two ventral valves, GSC 115545, 115546, $\times 1$. 3.5, ventral valve of *Sokolskya* sp., GSC 115547, $\times 1$. 3.6, ventral valve of *Chonetinella* cf. *C. jeffordsi* Stevens, 1962, GSC 115548, $\times 1$. 3.7–3.13, *Hystericulina* cf. *H. wabashensis* (Norwood and Pratten, 1855); 3.7, 3.8, ventral and dorsal views of an articulated specimen, GSC 115549; 3.9, natural mold of dorsal exterior, GSC 115550; 3.10–3.13, ventral, anterior, posterior, and lateral views of ventral valve, GSC 115551, all $\times 1.5$. 3.14–3.29, *Lazarevia stepanowensis* n. sp.; 3.14–3.19, ventral, dorsal, dorsal mold, anterior, posterior, and lateral views of the holotype, GSC 115552; 3.20–3.23, lateral, ventral, anterior, and posterior views of a large ventral valve paratype, GSC 115553; 3.24–3.27, ventral, anterior, posterior, and lateral views of a nearly complete paratype with a portion of the dorsal mold exposed, GSC 115554; 3.28, 3.29, ventral and posterior views of a natural mold paratype of the ventral interior showing muscle field, GSC 115555; all $\times 1$.

are significantly younger than *P. kalashnikovi*, ranging from Late Moscovian to Kasimovian in age.

Brunton et al. (1994) recently redescribed the type species of the chonopectinid genus *Semenewia* Paeckelmann, 1931. This genus is similar to *Plicatiferina* in having a flattened, regularly rugose "bauplan" with well-developed interareas in both valves and a row of spines at the hingeline. The surface is finely striate or capillate. Internally, the bilobed cardinal process is supported by a median septum. No radial micro-ornament has been observed in either the Hare Fiord Formation or Ladrones Limestone specimens which are of similar age. If the dorsal interior of the Ladrones specimen described above can be assumed to also typify the Hare Fiord Formation, it is safe to say that these late Bashkirian or early Moscovian specimens do not belong in *Semenewia*.

Distribution.—GSC locality C-5202 (34 specimens); GSC locality 56430A (two specimens). This species, or one very similar to it, occurs in collections of the Ladrones Limestone of southeastern Alaska. This material was collected in 1918 by G. H. Girty of the U. S. Geological Survey.

Suborder Productidina Waagen, 1883
 Superfamily Productoidea Gray, 1840
 Family Productellidae Schuchert, 1929
 Subfamily Productininae Muir-Wood and Cooper, 1960
 Tribe Paramarginiferini Lazarev, 1986
 Genus *Eomarginiferina* Brunton, 1966
?Eomarginiferina sp.
 (Fig. 6.11–6.15)

Comments.—These two specimens differ from the species described below as *Eomarginifera* in their narrower subtrigonal outline, similar to that seen in the genus *Eomarginiferina* Brunton. The mold of the dorsal exterior has the characteristic concave grooves delineating the ears that indicate the presence of a strong ridge wrapping around the ears of the dorsal valve interior. Unfortunately, one ear of the ventral valve is missing and the other is spalled making it impossible to determine whether or not there were halteroid spines on the ears. For this reason the assignment to *Eomarginiferina* is queried. Furthermore, this genus is not known above the Viséan.

Distribution.—GSC locality C-5202 (one ventral valve, one dorsal valve mold).

→

Fig. 4.—Productoids. 4.1–4.6, *?Retimarginifera* sp., ventral, dorsal, mold of dorsal exterior, lateral, anterior, and posterior views, GSC 115556, $\times 1.5$. 4.7–4.23, *Rugivestis pristina* n. sp.; 4.7, mold of dorsal exterior paratype, GSC 115557; 4.8–4.19, lateral, ventral, anterior, and posterior views of three ventral valves, GSC 115558–115560, respectively, including the holotype (GSC 115558) and two paratypes; 4.20–4.23, ventral, dorsal, partial dorsal exterior mold, and lateral views of a nearly complete specimen, GSC 115561; all $\times 1.5$. 4.24–4.43, *Maemia gelida* n. sp.; 4.24–4.28, ventral, dorsal, mold of dorsal exterior, posterior, and lateral views of the large holotype, GSC 115562; 4.29–4.31, ventral, dorsal, and mold of dorsal exterior of a small paratype, GSC 115563; 4.32–4.43, ventral, anterior, posterior, and lateral views of three ventral valve paratypes, GSC 115564–115566, respectively; all $\times 2$.

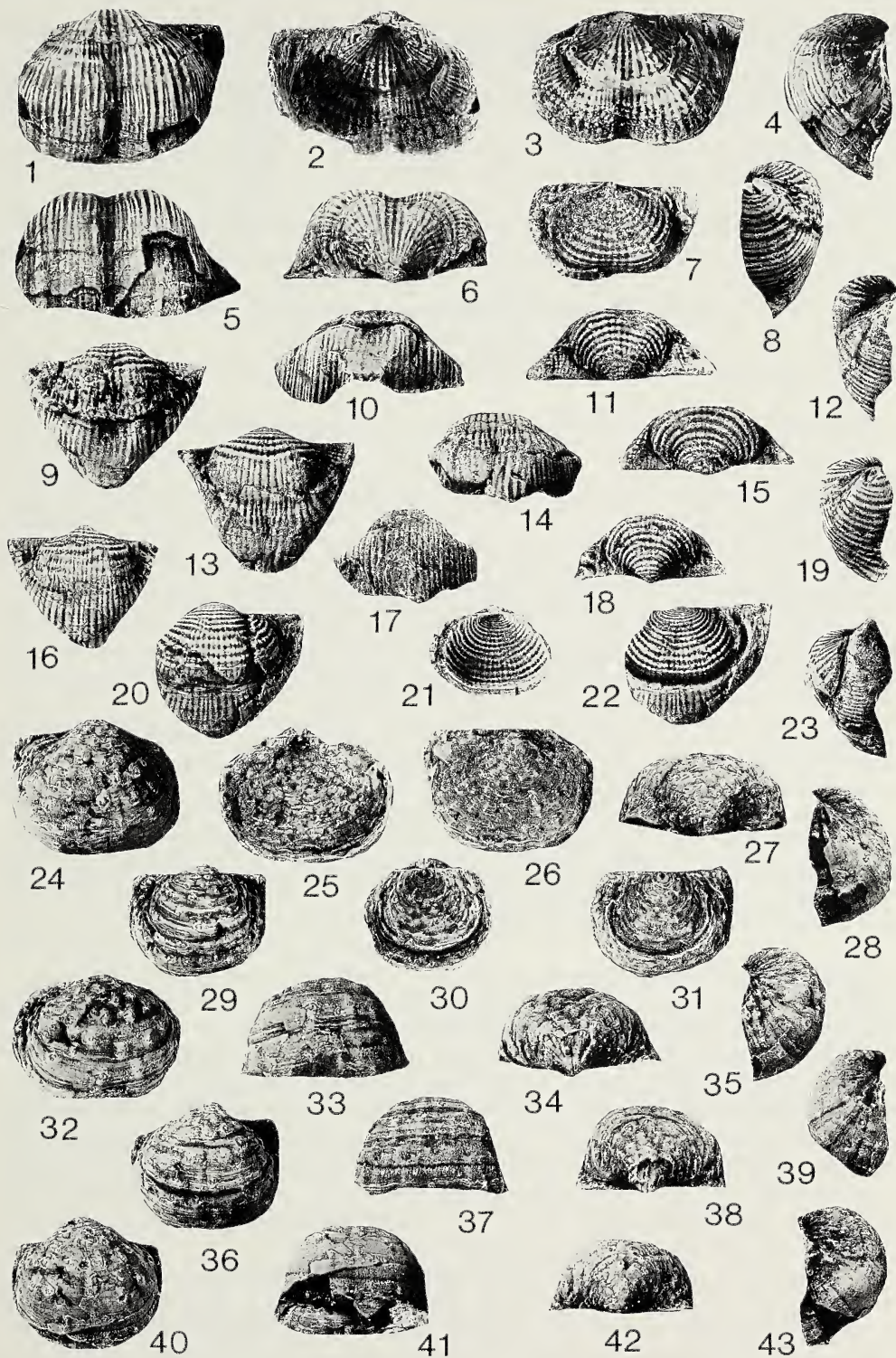


Table 5.—*Measurements (in millimeters) of the types of Rugivestis pristina n. sp. from GSC localities 56430 and 56430A.*

GSC number	Length	Width	Height	Surface length
115558	14.9	18.8	8.5	21.8
115559	14.8	18.4	6.7	21.3
115560	12.6	15.0	7.1	19.9
115561	14.0	—	6.9	20.2

Genus *Rugivestis* Muir-Wood and Cooper, 1960
Rugivestis pristina, new species
(Fig. 4.7–4.23)

Holotype.—GSC 115558, Figures 4.8–4.11, from GSC locality 56430.

Paratypes.—GSC 115557, Figure 4.7, GSC locality 56430A; 115559, Figures 4.12–4.15, GSC locality 56430A; 115560, Figures 4.16–4.19, from GSC locality 56430; 115561, Figures 4.20–4.23, from GSC locality 56430A.

Description.—Medium size for genus, transversely trigonal in outline; maximum width at hingeline; both valves strongly geniculate; body cavity thin; lateral profile moderately inflated, subangular.

Ventral valve with visceral disc wider than long, evenly and moderately convex, abruptly delimited from trail by strong cincture; ears large, flattened, weakly costellate, lacking rugae, defined by abrupt straight posterolateral vertical cincture of visceral disc; cardinal extremities formed as vertical flanges at 90-degree angle to ventral surface of ears; trail long and commonly anteriorly nasute; trail may be rounded, flattened, or have shallow sulcus posteriorly; visceral disc, excluding ears, reticulate, ornamented by moderately coarse rugae and moderately strong costellae, about seven to ten in five mm, commonly seven or eight; rugae abruptly terminate at ear ridges; trail with costellae only; spines rare, commonly with one or two pairs symmetrically arranged on visceral disc and one or more others scattered on visceral disc; spines on trail not observed; interior unknown.

Dorsal valve moderately concave; ears defined by straight posterolateral ridge as in opposite valve; trail short; anterior portion of visceral disc and trail with low fold; small protегulal node at hingeline; ornament of visceral disc similar to opposite valve; cincture absent on exterior molds; spines on dorsal visceral disc not observed; interior poorly known, with lateral ridges diverging from hingeline and presumably following cincture; other details not observed.

Measurements.—See Table 5.

Diagnosis.—This species is characterized by moderate size, coarse ribbing, nonrugose ears, and moderately nasute trail.

Comments.—*Rugivestis pristina*, n. sp., is similar in most respects to both *Rugivestis carinata* (Muir-Wood and Cooper, 1957), the type species, and *R. kutorgae* (Chernyshev, 1902). The former, of Middle Permian age, is smaller and has a ventral sulcus on the ventral visceral disc, a narrowly nasute trail, and weakly rugose ears. The latter, of Asselian or Early Permian age, is considerably larger and most specimens are not nasute. In addition the ears are proportionately smaller and bear good rugae. The genus is quite rare and the dorsal interior is still unknown so far as we know.

Distribution.—GSC locality 56430 (four ventral valves); GSC locality 56430A (four ventral valves, one mold of dorsal exterior, two partially bivalved specimens); GSC locality C-4087 (one ventral valve). This species, or one very similar to it, also occurs in the Ladrone Limestone of southeastern Alaska.

Table 6.—Measurements (in millimeters) of ?*Fimbrinia borealis* n. sp. from GSC locality 56430.

GSC number	Valve	Length	Width	Height	Surface length
115582	ventral	11.1	10.6	5.4	17.0
115583	ventral	10.0	10.9	4.8	14.3
115584	dorsal	8.5	11.2	4.6	—

Subfamily Overtoniinae Muir-Wood and Cooper, 1960

Tribe Overtoniini Muir-Wood and Cooper, 1960

Genus *Fimbrinia* Cooper, 1972

?*Fimbrinia borealis*, **new species**

(Fig. 6.33–6.43)

Holotype.—GSC 115582, Figures 6.33–6.36, a ventral valve, from GSC locality 56430.

Paratypes.—GSC 115583 and 115584, Figures 6.39–6.43, a ventral valve and a natural mold of the dorsal exterior, from same locality as holotype.

Description.—Small; strongly concavoconvex, body cavity thin; outline subovate; greatest width usually at hingeline, rarely at midlength; lateral profile subguttate to subovate; anterior profile bell-shaped.

Ventral valve strongly inflated posteriorly, most convex in umbonal region; beak small, scarcely overhanging hingeline; venter well rounded in both views, flanks sloping steeply to lateral margins; ears of moderate size, subangular, well defined by concave flexures; trail moderately convex; entire surface strongly rugose and thickly lamellose with strong, moderately broad, irregular rugae; spine bases nearly regularly spaced, arranged in concentric rows along crests of rugae; interior unknown.

Dorsal valve strongly concave; most concave posteriorly; ears delimited by convex flexures; very small protegular node present at midhingeline; trail absent; ornament consisting of strong lamellose rugae only; spines and dimples apparently absent; interior unknown.

Measurements.—See Table 6.

Diagnosis.—This species is characterized by its small size, rounded outline, strongly convex venter, tumid profile, and coarse rugose ornament on both valves.

Comments.—The dorsal valve of this species is poorly known. The two specimens at hand are spalled dorsal interiors and do not give any indication of the presence of spines or dimples on the exterior surface as one would expect in the genus *Fimbrinia*. However, the state of preservation of these specimens is far from perfect and we cannot discount the possibility that the true ornament is not fully expressed in these specimens.

This species cannot be assigned to a genus or even family with confidence. The strong rugae on both valves, especially the dorsal valve, are unusual for the genus *Fimbrinia* or, for that matter, *Overtonia*. The apparent absence of dorsal spines is even more troubling. Assignment to the genus *Fimbrinia* is a name choice of convenience, for this species must have a genus name. Its distinctive shape, profile, and ornament are reason enough to propose a new species but we have little idea as to its true congeners.

Distribution.—GSC locality 56430 (five ventral valves, two dorsal valves).

Tribe Krotoviini Brunton, Lazarev and Grant, 1995

Genus *Krotovia* Frederiks, 1928

Krotovia cf. *K. spinulosa* (J. Sowerby, 1814)

(Fig. 6.31, 6.32)

1814 *Productus spinulosus* J. Sowerby, p. 155, pl. 68, fig. 3.

Description.—Medium size; outline subcircular to slightly transversely subovate; ventral valve mod-

erately and almost evenly convex, most convex in umbonal region; umbonal region moderately inflated, narrow, moderately incurved; beak small, slightly overhanging hingeline; ornament of weak, closely spaced rugae, strongest near sides of umbo, and concentric rows of round, small, tubercular spine bases crudely arranged in quincunx; widely spaced growth lamellae rarely preserved; spines apparently erect; other details unknown.

Comments.—This Arctic species conforms fairly closely to Brunton's (1966) redescription of *Krotovia spinulosa* (J. Sowerby) from the Upper Viséan of Ireland. It differs mainly in having stronger rugation and a slightly narrower umbonal region.

Distribution.—GSC locality 56430 (three ventral valves).

Krotovia cf. *K. lamellosa* Brunton, 1966
(Fig. 6.28–6.30)

1966 *Krotovia lamellosa* Brunton, p. 225, pl. 13, fig. 8–16; pl. 14, fig. 1–19.

Description.—Small, outline subcircular; ventral umbonal region strongly inflated, narrow, strongly incurved; beak small, overhanging hingeline; ornament consisting only of lamellose growth lamellae; fine spines of variable size arranged in concentric rows on growth lamellae; other details not observed.

Comments.—This solitary specimen agrees in most respects with Brunton's (1966) description and illustrations of *Krotovia lamellosa* from the Upper Viséan of Ireland. It differs only in having fewer spines on the growth lamellae.

Distribution.—GSC locality 56430 (one ventral valve).

Subfamily Marginiferinae Shehli, 1954
Tribe Paucispiniferini Muir-Wood and Cooper, 1960
Genus *Hystriculina* Muir-Wood and Cooper, 1960
?Hystriculina cf. *H. wabashensis* (Norwood and Pratten, 1855)
(Fig. 3.7–3.13)

1855 *Productus wabashensis* Norwood and Pratten, p. 13, pl. 1, fig. 6a–d.

Description of Hare Fiord Specimens.—Small, strongly concavoconvex; outline of visceral disc subquadrate; greatest width at hingeline; both valves moderately geniculate; cardinal extremities subangular; lateral profile nearly semicircular; anterior profile subquadrate to subtrapezoidal; shell substance thin.

Ventral valve strongly inflated, most convex at point of geniculation; visceral disc only moderately convex; flanks dropping steeply to lateral margins; cardinal extremities well defined by concave flexures; beak small, projecting posteriorly slightly beyond hingeline; umbonal region not much inflated, subtending an angle of about 90 to 100 degrees; sulcus well developed, originating on anterior half of visceral disc, becoming deeper and extending to anterior margin; ornament on visceral disc consisting of moderately strong, nearly regular, low rugae on whole visceral disc and weak costae anteriorly; flanks and venter with numerous low, rounded, variably strong costellae, about seven to eight per five mm near point of geniculation; erect spine bases sparsely scattered on visceral disc and trail, several finer spines in row along hingeline; interior not observed.

Dorsal valve weakly concave in visceral disc; cardinal extremities well set off by convex flexures; sulcus originating in anterior third of visceral disc; ornament consisting of weak rugae and scattered, rounded pits on visceral disc; ribbing on trail complementary to opposite valve; spines apparently absent; interior not observed.

Comments.—This genus has heretofore been restricted to much younger horizons and the generic identification should be viewed with caution. These Hare Fiord specimens differ little externally from the specimens of *H. wabashensis* illustrated by Sturgeon and Hoare (1968) from the Ames Limestone (Upper Missourian) of Ohio. The ears of this Arctic species are considerably smaller than on those illustrated by Dunbar and Condra (1932) from the Missourian and Virgilian of Nebraska.

Distribution.—GSC locality 56430 (16 specimens); GSC locality 56430A (one ventral valve).

Genus *Retimarginifera* Waterhouse, 1970

?*Retimarginifera* sp.

(Fig. 4.1–4.6)

Description.—Small to medium size; strongly concavoconvex; body cavity thin; outline subquadrate; maximum width at hingeline; ears medium size, not large; visceral disc strongly geniculated; trail moderately long.

Ventral valve strongly inflated; sulcus well developed, originating in umbonal region, becoming uniformly deeper and wider over much of valve; angular ears defined by concave flexures; visceral disc weakly convex, most convex near beak, weakly reticulate with few irregularly spaced rugae intersected by numerous simple or bifurcating fine costae on anterior portion; trail with moderately strong costae, about eight to ten per five mm; spines sparsely distributed, with single strong spine on ears, pair of strong spines on sides of umbo, and few fine spines on umbo and near hingeline; interior unknown.

Dorsal valve strongly concave; fold originating in umbonal region; ears well delimited by abrupt convex flexures; ornament complementary to opposite valve but with few rounded pits on visceral disc; spines absent; interior unknown.

Comments.—This species is represented in the Hare Fiord by only one nearly complete specimen. Another poorly preserved ventral valve may belong here as well. The lack of a dorsal marginal ridge or multiple trails eliminates it from the Marginiferinae. There is superficial similarity to the Late Carboniferous genus *Jiguliconcha* Lazarev, 1990, but that genus has weak, fine ribbing, and no halteroid spines on the ears or umbo, but it does have a row of spines on the lateral slopes unlike the Hare Fiord specimen. The modest size, thin body cavity, weakly reticulate visceral disc, paired halteroid spines at the ears and umbo suggest placement in the subfamily Hystriculinae. Assignment within this subfamily is difficult. The Permian genus *Retimarginifera* Waterhouse is similar in most respects but has a much more strongly reticulate visceral disc. Therefore we assign it here with considerable uncertainty.

Distribution.—GSC locality C-5202 (one ventral valve); GSC locality 56430 (one ventral valve).

Subfamily Plicatiferinae Muir-Wood and Cooper, 1960

Tribe Plicatiferini Muir-Wood and Cooper, 1960

Genus *Lazarevia*, new genus

Type Species.—*Lazarevia stepanowensis*, n. sp.

Derivation of Name.—Named in honor of the productid brachiopod specialist S. S. Lazarev.

Diagnosis.—Large for tribe, outline transverse; both valves with vertical flanges at cardinal extremities; ornament consisting of weak, irregularly spaced rugae on visceral disc, and numerous uniform costae on trail and anterior portion of visceral disc, forming weak reticulation on anterior portion of disc; fine spine bases scattered sparsely over surface of ventral valve; row of several fine spines close to hingeline on each side of umbo; row of erect spine bases wrapping around ears to posterolateral margins; dorsal spines absent; ventral interior with low rim of thickened shell matter extending around auricularia and near anterior and lateral margins of valve.

Comments.—This new genus is most similar to, and possibly derived from, the Viséan genus *Plicatifera* Chao, 1927. It differs in having much weaker, more

irregular rugae, a shorter trail, more numerous spines on the ventral valve with a row along the hingeline and another row wrapping around the ears to the posterolateral margins. Internally, there is a low rim extending around the whole ventral valve. *Plicatifera* has strong, regular rugae on the visceral disc and a moderately long, well-developed trail. The ventral interior seems to lack the thickened rim seen in *Lazarevia* and the spine distribution is much different. Other members of this tribe, such as *Ferganoproductus* Galitzkaya, 1977 and *Rugoconcha* Jin and Sun, 1981, can be differentiated by the following characters. *Ferganoproductus* has irregular wavy rugae on the visceral disc, lacks costae, and has numerous elongated spine tubercles crudely arranged in quincunx on the ventral valve. It also may have strong, erect spines on the dorsal valve. *Rugoconcha* is based on *Plicatifera chaoi* Grabau, 1936, but the few poor photographs available show specimens that seem more similar to *Plicatiferina* Kalashnikov than *Plicatifera* Chao. It has strong, regular, numerous rugae over the entire surface, lacks ribs, seems to lack a trail, and has scattered spine bases. The dorsal valve appears to be unknown as does ventral valve morphology as seen from a dorsal view.

Distribution.—Late Bashkirian to early Moscovian of Ellesmere Island, Canadian Arctic Archipelago.

Species Assigned.—Monotypic.

Lazarevia stepanowensis, new species
(Fig. 3.14–3.29)

Holotype.—GSC 115552, Figures 3.14–3.19, a nearly complete specimen from GSC locality 56430.

Paratypes.—GSC 115553, Figures 3.20–3.23, a ventral valve; GSC 115554, Figures 3.24–3.27, both valves partially preserved; GSC 115555, Figures 3.28 and 3.29, natural mold of ventral interior; all from GSC locality 56430.

Description.—Outline transversely semicircular to subovate; maximum width at or slightly anterior to hingeline; strongly concavoconvex with thin body cavity; lateral profile subsemicircular, evenly convex.

Ventral valve strongly and almost evenly convex in lateral profile; venter flattened or with weak sulcus; ears of moderate size, subangular, defined by concave flexures ventrally and nearly vertical gutterlike flanges laterally; lateral slopes moderately convex; umbonal region broad, weakly inflated; beak small; ornament consisting of numerous low, fine, irregularly spaced rugae on visceral disc and numerous fine, mostly regular costae or coarse costellae that originate on anterior portion of visceral disc and extend to anterior margin, about six or seven in five mm at 20-mm surface measure from beak; fine spine bases scattered sparsely over surface; row of several (four or more) fine spines very close to hingeline on each side of umbo; row of seven or eight erect spine bases wrapping around ears to posterolateral margins; interior smooth, lacking shagreen, in umbonal region; with low rim, strongest at auricularations, that extends around entire visceral disc except for umbo, producing weak cincture in spalled specimens; adductor scars chordate, posteriorly placed in umbonal region, moderately impressed; diductors not impressed, poorly delimited, weakly striate.

Dorsal valve slightly less convex than opposite valve; gutterlike flanges at cardinal extremities similar to those of opposite valve; small, prominent protugal node at posteromedial margin; fold, if present, weak and originating on anterior portion of visceral disc; ornament similar and complementary to ventral valve but weaker; spine bases not present; interior with small, sessile, bilobed cardinal process, short, thin median septum that extends forward from near base of cardinal process to about half length of visceral disc, moderately developed lateral ridges that diverge from hingeline at low angle extending about halfway toward auricularations, and numerous strong endospines anteriorly; other internal details unobserved.

Measurements.—See Table 7.

Comments.—This Arctic species bears some superficial resemblance to species

Table 7.—Measurements (in millimeters) of *Lazarevia stepanowensis* n. sp. from GSC locality 56430.

GSC number	Length	Width	Height	Surface length
115552	22.3	32.6	14.2	35.3
155553	25.3	40.0	16.5	39.0
115554	24.3	39.0	15.8	36.2

of the genus *Desmoinesia* Hoare but can readily be differentiated from that genus by its larger size, more transverse outline, lack of dorsal spines, the presence of lateral flanges, and a weak cincture on spalled surfaces of the ventral valve that reflects a low thickening or rim that extends around the interior of the ventral valve.

Plicatifera pseudoplicatilis (Muir-Wood), as illustrated in Brunton et al. (1993), is similar in size, transverse outline, and general ornament but differs in having much stronger and more regular rugae, a longer trail, and an almost completely reticulate visceral disc.

Distribution.—This species is common at GSC locality 56430 (90 specimens).

Tribe Semicostellini Nalivkin, 1979

Genus *Maemia* Lazarev, 1997

Maemia gelida, **new species**

(Fig. 4.24–4.43)

Holotype.—GSC 115562, Figures 4.24–4.28, from GSC locality C-5202.

Paratypes.—GSC 115563–115566, Figures 4.29–4.43, from GSC locality C-5202.

Description.—Small, nearly planoconvex; outline transversely subovate; greatest width at about midlength, rarely at hingeline; ears small, compressed, subangular; anterior profile subsemicircular to rounded subtrapezoidal; lateral profile subsemicircular.

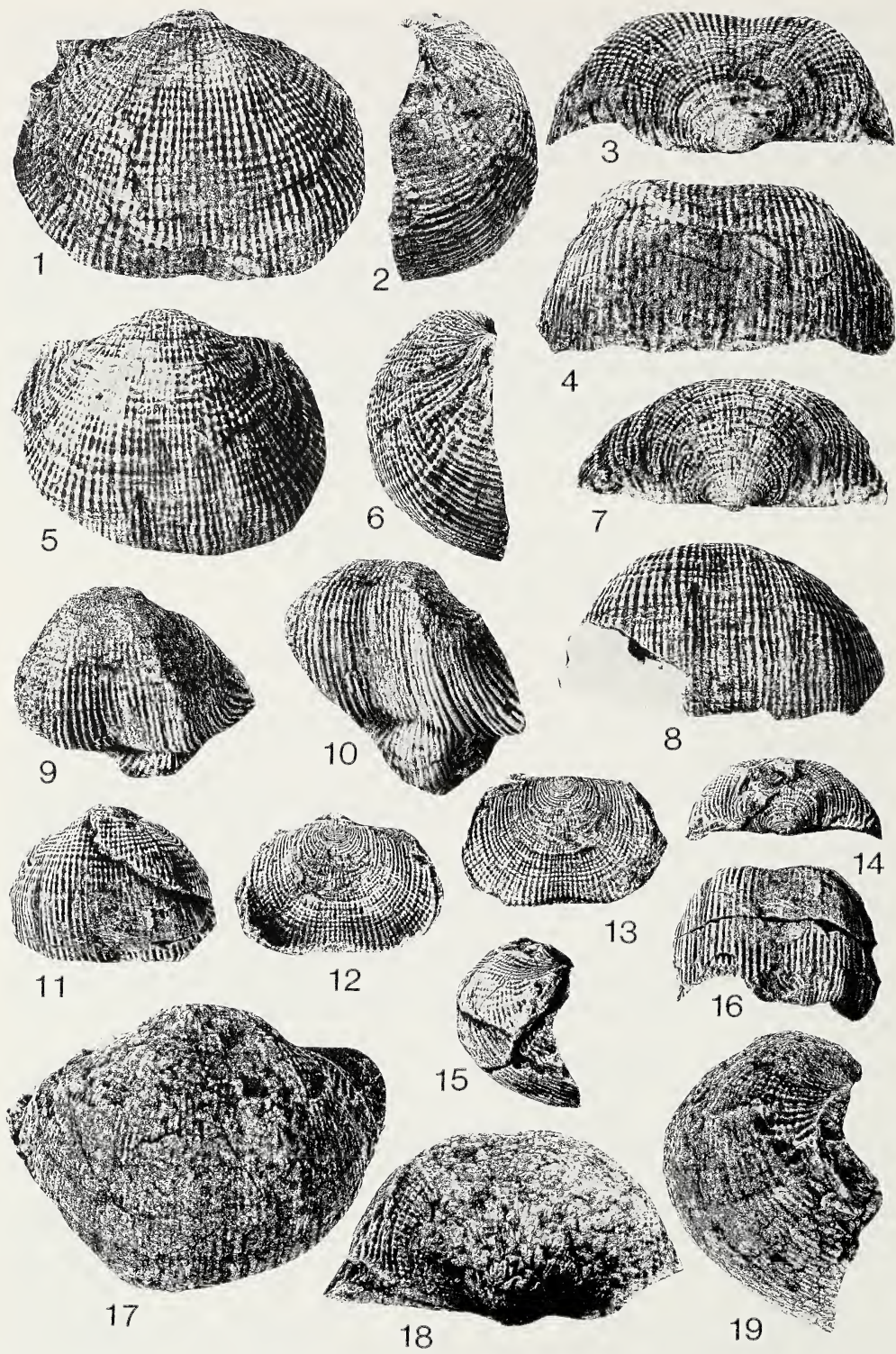
Ventral valve strongly inflated, evenly convex except for more convex umbonal region; visceral disc not delineated; venter weakly convex, flanks dropping steeply to lateral margins; trail very short, not well defined; ears set off by deeply concave flexures; umbonal region weakly inflated and of moderate width; beak small, slightly overhanging hingeline; entire valve weakly and irregularly rugose and slightly lamellose, each strong concentric stricture anterior to strong rugae indicating former position of dorsal visceral disc; coarse, slightly elongate nodular spine bases or tubercles arranged crudely in quincunx over most of valve; finer, more numerous spines on ears, on sides of umbo, and near hingeline; interior not observed.

Dorsal valve almost flat or very weakly concave, except for very short, sharply geniculated trail; small medial protegular node present; ornament consisting of weaker rugae than those of opposite valve and scattered shallow dimples; numerous fine, scattered spine bases present; interior not observed.

Measurements.—See Table 8.

Table 8.—Measurements (in millimeters) of the types of *Maemia gelida* n. sp. from GSC locality C-5252.

GSC number	Length	Width	Height	Surface length
115562	10.2	13.0	6.1	16.9
115563	8.5	10.6	5.4	13.4
115564	9.9	12.3	6.6	17.2
155565	9.5	11.5	6.7	16.1
115566	10.1	11.5	6.5	17.5



Diagnosis.—The combined characters of a rugose, spinose, noncostate ornament and flat, spinose dorsal valve with very short trail characterize this species.

Comments.—Despite the small size of this new species its general morphology suggests that it is closely related to the recently described genus *Maemia* Lazarev. The type species of that genus, *Maemia chaykensis* Lazarev, 1997 (in Brunton and Lazarev, 1997), however, is much larger and bears a shallow ventral sulcus and coarse costae on the trail. Another species from the same horizon at Cape Chaika, *Maemia nana* Lazarev, however, is similar to this Canadian species in size and ornament. It differs in having much weaker spine base tubercles and weak, coarse ribbing on the ventral valve.

Distribution.—GSC locality C-5202 (25 specimens); GSC locality 56430 (six specimens).

Family Productidae Gray, 1840

Subfamily Dictyoclostinae Stehli, 1954

Genus *Reticulatia* Muir-Wood and Cooper, 1960

Reticulatia cf. *R. americanus* (Dunbar and Condra, 1932)

(Fig. 5.1–5.8)

1932 *Dictyoclostus americanus* Dunbar and Condra, p. 218, pl. 34, fig. 3–6.

Description.—Large, moderately concavoconvex; outline transversely subovate to subquadrate; maximum width probably near hingeline (ears incomplete in all specimens); lateral profile subsemicircular; anterior profile subtrapezoidal; fold and sulcus moderately developed; body cavity moderately thick.

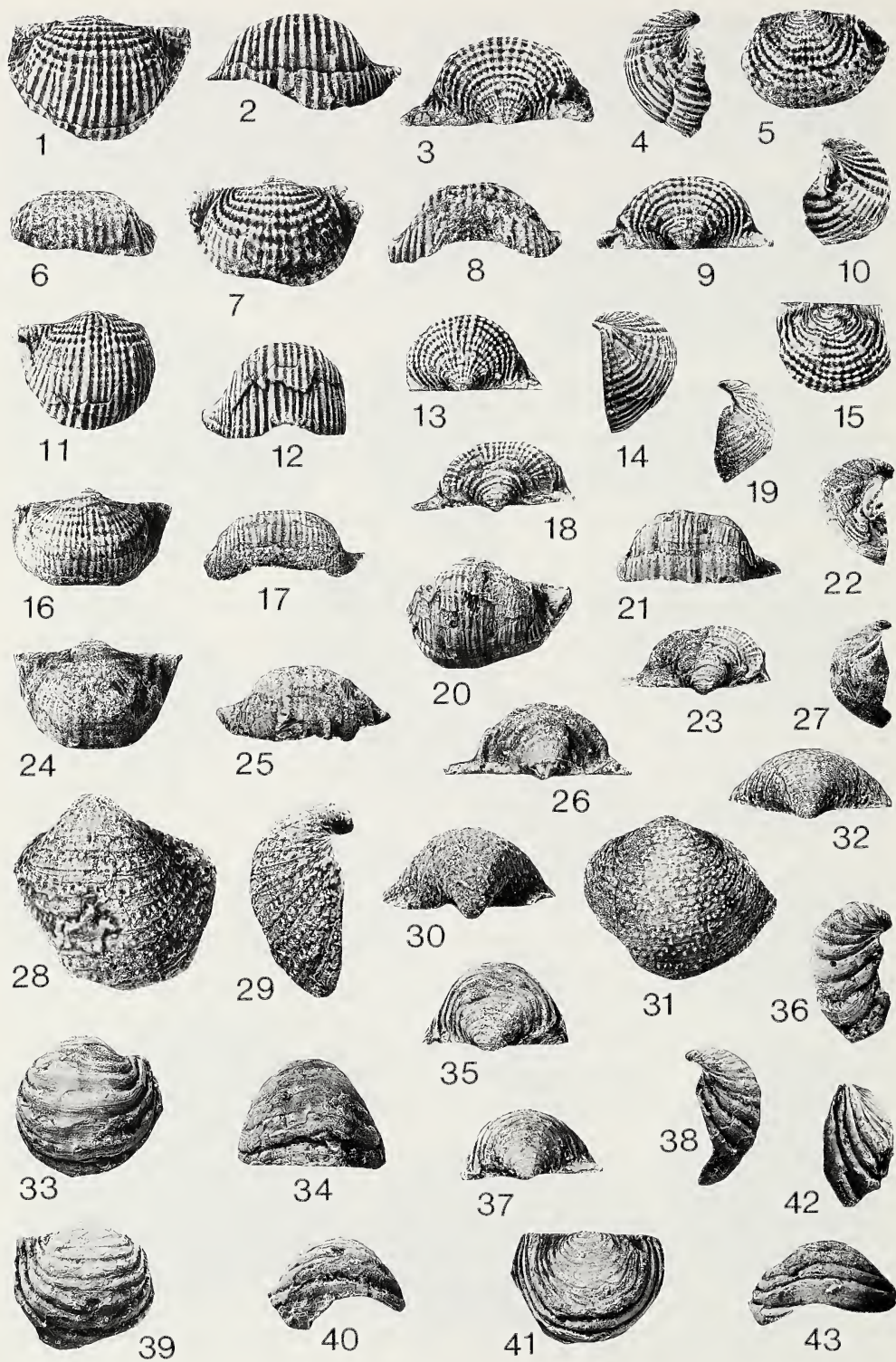
Ventral valve moderately inflated, almost evenly convex, most convex near beak; umbo broad, moderately produced, subtending an angle well in excess of 90 degrees; beak small, slightly overhanging hingeline; flanks moderately convex, sloping steeply to lateral margins; rounded sulcus originating in umbonal region, remaining shallow, sometimes obscure, throughout entire length; ears delimited by concave flexures, not fully preserved; visceral disc delineated by weak geniculation and loss of reticulate ornament; ornament of visceral disc strongly and regularly reticulate with numerous, almost regular rugae intersecting regular coarse costae, about four or five per five mm on anterior portion of visceral disc; spine bases found in row along hingeline, around ears, and scattered elsewhere; interior unknown.

Dorsal valve moderately concave, geniculate; fold low throughout; ears delimited by convex flexures; trail not well preserved; ornament of visceral disc complementary to opposite valve; no spines observed; interior unknown.

Comments.—These incomplete Arctic specimens agree in most observable details with typical *Reticulatia americanus* (Dunbar and Condra), of Missourian or Kazimovian age of Nebraska and surrounding environs. The latter differs little from the Hare Fiord specimens, mainly in having numerous spines scattered on the trail. Muir-Wood and Cooper (1960) emphasized the well-developed ginglymus in this genus, a character not preserved in our specimens. The trail also is broken in all of our specimens. Therefore, identification is tentative.

←

Fig. 5.—Productoids. 5.1–5.8, *Reticulatia* cf. *R. americanus* (Dunbar and Condra, 1932), ventral, lateral, posterior, and anterior views of two ventral valves, GSC 115567 and 115568, $\times 1$. 5.9–5.16, *Kutorginella* cf. *K. mosquensis* Ivanova, 1951; 5.9, 5.10, ventral and oblique views of ventral valve with siphon, GSC 115569; 5.11–5.16, ventral, dorsal, mold of a dorsal exterior, posterior, lateral, and anterior views of a small complete specimen, GSC 115570; both $\times 1$. 5.17–5.19, *Antiquatonia* cf. *A. hermosana* (Girty, 1903), ventral, posterior, and lateral views of a ventral valve showing the spine ridge on the right ear, GSC 115571, $\times 1$.



Distribution.—GSC locality 60194 (two ventral valves and two articulated specimens).

Tribe Kozlowskiini

Genus *Eomarginifera* Muir-Wood, 1930

Eomarginifera sp.

(Fig. 6.1–6.10)

Comments.—This species is assigned to *Eomarginifera* on the basis of having three pairs of halteroid spines on the ears, umbo, and trail of the ventral valve. Deep concave grooves defining the ears indicate that there are strong lateral ridges curving around the ears in the dorsal valve as in *Eomarginifera*. A large fragment of conjoined valves shows the trails of both valves touching each other at the anterior margin, obviating the possibility that this species could be assigned to *Kozlowskia* which has numerous short trails bunched at the anterior margin. The transverse outline and widely spaced pair of halteroid spines on the trail demonstrate that it cannot be assigned to *Eomarginiferina* Brunton, 1966.

Assignment to a species of *Eomarginifera* is more difficult. The coarse ribs and rounded venter of this Arctic species are not usual for the genus *Eomarginifera*. Externally, the ventral valves resemble the species described as *Kozlowskia* sp. by Lazarev (1990:pl. 21, fig. 24b, v), of Moscovian age from the Moscow Basin.

Distribution.—GSC locality 56430 (five ventral valves, two dorsal valve molds, one fragment of conjoined valves); GSC locality C-5202 (one ventral valve).

Genus *Kozlowskia* Frederiks, 1933

?*Kozlowskia splendens* (Norwood and Pratten, 1855)

(Fig. 6.16–6.27)

1855 *Productus splendens* Norwood and Pratten, p. 11, pl. 1, fig. 5a–d.

Description.—Small; outline transversely subsemicircular to subtrapezoidal; greatest width at hinge-line; lateral profile subtrigonal to subsemicircular; anterior profile subtrapezoidal to subsemicircular.

Ventral valve strongly inflated with moderately convex visceral disc and less convex geniculated trail; ears large, slightly mucronate or compressed, well delineated by concave flexures; venter rounded to flattened or weakly sulcate; flanks steeply sloping to lateral margins; radial ornament of low, weak costellae, confined to trail and that portion of visceral disc anterior to umbonal region; visceral disc with weak rugae, forming weakly reticulate pattern near point of geniculation; three pairs of halteroid spines at ears, sides of visceral disc, and on trail; few finer spine bases scattered near hingeline and on umbo; interior unknown.

Fig. 6.—Productoids. 6.1–6.10, *Eomarginifera* sp.; 6.1–6.4, 6.7–6.10, ventral, anterior, posterior, and lateral views of two ventral valves, GSC 115572 and 115573; 6.5, 6.6, ventral and anterior views of natural mold of dorsal exterior, GSC 115574; all $\times 1.5$. 6.11–6.15, ?*Eomarginiferina* sp.; 6.11–6.14, ventral, anterior, posterior, and lateral views of ventral valve, GSC 115575; 6.15, ventral view of natural mold of dorsal exterior, GSC 115576; all $\times 1.5$. 6.16–6.27, ?*Kozlowskia splendens* (Norwood and Pratten, 1855), ventral, anterior, posterior, and lateral views of three ventral valves, GSC 115577–115579, respectively, $\times 1.5$. 6.28–6.30, ventral, lateral, and posterior views of *Krotovia* cf. *K. lamellosa* Brunton, 1966, GSC 115580, $\times 3$. 6.31, 6.32, ventral and posterior views of *Krotovia* cf. *K. spinulosa* (J. Sowerby, 1814), GSC 115581, $\times 3$. 6.33–6.43, ?*Fimbrinia borealis* n. sp.; 6.33–6.40, ventral, anterior, posterior, and lateral views of two ventral valves, including the holotype (6.33–6.36), GSC 115582 and 115583; 6.41–6.43, ventral, lateral, and anterior views of a mold of the dorsal exterior, GSC 115584; all $\times 2$.

Dorsal valve known only from external molds. Trail sharply geniculated; ears smaller than opposite valve; visceral disc flattened, weakly convex; ornament as in opposite valve but weaker; spines absent; evidence of numerous trails lacking; interior unknown.

Comments.—The large ears, variably developed fold, and obsolescent costellae on the trail characterize these Hare Fiord specimens. In this respect these Arctic specimens are virtually indistinguishable from typical specimens of *Kozlowskia splendens* from Desmoinesian and Missourian beds in the midcontinent, an admittedly highly variable species according to Dunbar and Condra (1932).

The absence of specimens that indicate the presence of a sheaf of closely packed short trails at the dorsal margin is unfortunate. If there is no dorsal rim of numerous trails this species is not a *Kozlowskia* and might be reassigned to another genus such as *Eomarginiferina* Brunton, 1968. However, the weak reticulation and anterior ribbing in this Arctic species are more suggestive of *Kozlowskia* than *Eomarginiferina*.

Distribution.—GSC locality 56430 (six ventral valves); GSC locality 56430A (five ventral valves).

Tribe Retariini Muir-Wood and Cooper, 1960

Genus *Kutorginella* Ivanova, 1951

Kutorginella cf. *K. mosquensis* Ivanova, 1951

(Fig. 5.9–5.16)

1951 *Kutorginella mosquensis* Ivanova, p. 329.

Description.—Medium size; outline subquadrate; lateral profile strongly inflated, subtrapezoidal; anterior profile subquadrate to subtrapezoidal; point of maximum width apparently anterior to hinge-line; ears small to medium; fold and sulcus moderately well developed, originating in umbonal region, becoming broader and deeper anteriorly; visceral disc reticulate with numerous rugae intersecting moderately strong costae; costae numbering about five or six in five mm on trail, extending forward over entire trail.

Ventral valve moderately geniculated; ears defined by concave flexures; lateral slopes dropping steeply to lateral margins; trail long with medial tube-like extension formed by distinctive stricture in largest specimen; spine bases scattered over umbonal region and trail with regular row wrapping around each ear; spines along hingeline not observed due to poor preservation; interior not observed.

Dorsal valve with flattened visceral disc and subquadrate outline; ears delimited by low convex flexures; dorsum with low fold; trail at least eight to ten mm long; ornament reticulate; spines absent; irregular rows of rounded pits on ears; interior unknown.

Comments.—The genus *Kutorginella* Ivanova ranges from the uppermost Serpukhovian to the Kungurian and many species have been described. These Hare Fiord specimens resemble *K. mosquensis* Ivanova from the Kazimovian of the Moscow Basin in ornament and development of an incomplete siphonal or tube-like trail extension in large, fully mature specimens. They also fall within the size range of specimens illustrated by Sarycheva (1971:pl. 5, fig. 1a, b) and Sarycheva and Sokolskaya (1952:pl. 37, fig. 230). However, they differ from the specimens illustrated by Sarycheva and Sokolskaya (1952) and Lazarev (1990:pl. 19, fig. 1) in being less transverse and the ears appear to be smaller, although these Hare Fiord specimens are not complete.

Distribution.—GSC locality 56430 (one ventral valve); GSC loc. 4085 (one specimen); GSC locality C-5202 (one ventral valve).

Genus *Antiquatonia* Miloradovich, 1945

Antiquatonia cf. *A. hermosana* (Girty, 1903)

(Fig. 5.17–5.19)

1903 *Productus semireticulatus* var. *hermosanus* Girty, p. 358, pl. 2, fig. 1–4.

Description.—Large, strongly inflated; outline subovate to subquadrate; widest at hingeline; ears

large, well defined; ventral sulcus narrow, shallow; visceral disc strongly reticulate, slightly geniculated from long trail; trail costate with about seven to nine costae per cm near anterior margin; ears set off by conspicuous ridge that wraps around ears; coarse spine bases sparsely scattered on trail and visceral disc; spines on ears and umbonal region obscured by poor preservation; other details not observed.

Comments.—The umbonal region of this single ventral valve is slightly crushed. Otherwise this specimen closely resembles the large ventral valve illustrated by Girty (1903:pl. 3, fig. 1–1c). Sutherland and Harlow (1973:pl. 11, fig. 6a–c) illustrated a smaller narrower specimen that otherwise is similar to this Arctic specimen.

Distribution.—GSC locality 56430 (one ventral valve).

Superfamily Echinoconchoidea
Family Echinoconchidae Stehli, 1954
Subfamily Pustulinae Waterhouse, 1981
Genus *Pustula* Thomas, 1914
?Pustula sp.
(Fig. 7.2)

Comments.—This single incomplete, slightly distorted ventral valve has mostly slightly elongate spine bases arranged in quincunx, with distinctive scattered, rounded pits between some of the spine bases. There are a few weak, irregular rugae, most noticeable around the ears. The low, rounded profile and vaguely rounded outline combined with this peculiar ornament suggest assignment to the genus *Pustula*, although that genus is more rugose and does not normally have rounded pits between the spine bases of the ventral valve.

Distribution.—GSC locality C-5202 (one ventral valve).

Subfamily Echinoconchinae Stehli, 1954
Tribe Echinoconchini Stehli, 1954
Genus *Echinaria* Muir-Wood and Cooper, 1960
?Echinaria sp.
(Fig. 7.1)

Comments.—A single large, partial echinoconchoid ventral valve seems likely to belong in the genus *Echinaria*. Although spine bases cannot be discerned, the shape and size of this specimen suggest assignment here, although a dorsal interior is needed for certain identification.

Distribution.—GSC locality 56430 (one partial ventral valve).

Superfamily Linoproductoidea Stehli, 1954
Family Monticuliferidae Muir-Wood and Cooper, 1960
Subfamily Auriculispinae Waterhouse, 1986
Genus *Liraria* Cooper and Grant, 1975
Liraria paucispina, **new species**
(Fig. 7.3–7.18)

Holotype.—GSC 115587, Figures 7.3, 7.11–7.14, a ventral valve, from GSC locality C-5202.

Paratypes.—GSC 115588, Figures 7.4, 7.15–7.18, a ventral valve; GSC 115589, Figures 7.5 and 7.6, a complete specimen with the visceral disc removed showing the mold of the dorsal exterior; GSC 115590, Figures 7.7–7.10, a large ventral valve; all from GSC locality C-5202.

Description.—Small to medium size; strongly concavoconvex; body cavity thin; outline subovate;

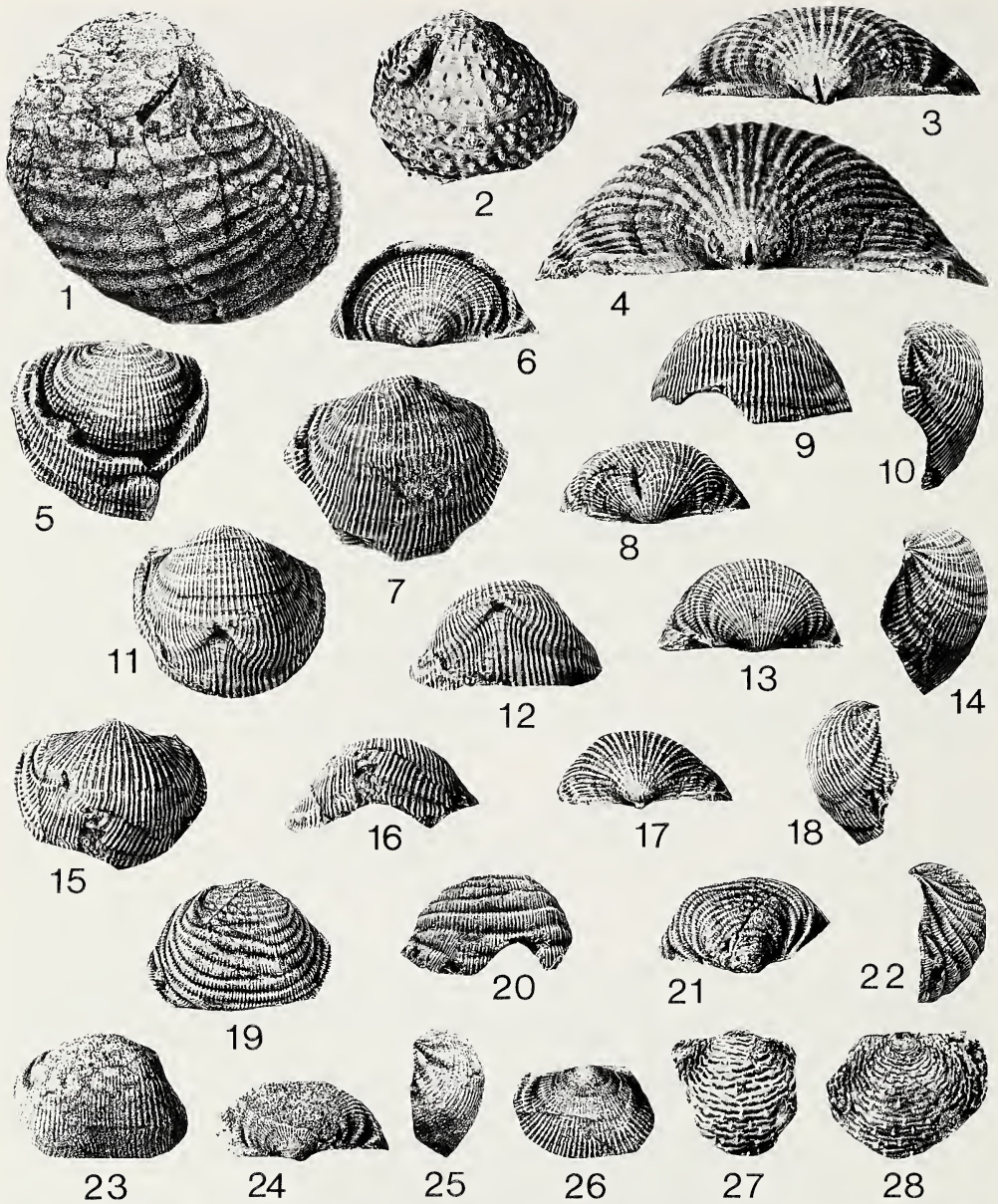


Fig. 7.—Productoids. 7.1, *?Echinaria*, ventral valve, GSC 115585, $\times 1$. 7.2, *?Pustula* sp., ventral valve, GSC 115586, $\times 2$. 7.3–7.18, *Liraria paucispina* n. sp.; 7.3, 7.11–7.14, ventral posterior view showing attachment scars and spine bases at hinge, $\times 4$, and ventral, posterior, anterior, and lateral views of the holotype, $\times 1.5$, GSC 115587; 7.4, 7.15–7.18, ventral posterior of a paratype showing attachment scars and spine bases at hinge, $\times 4$, and ventral, posterior, anterior, and lateral views of paratype GSC 115588, $\times 1.5$; 7.5, 7.6, ventral and posterior views of complete paratype with visceral disc removed, GSC 115589, $\times 1.5$; 7.7–7.10, ventral, posterior, anterior, and lateral views of a large ventral valve paratype, GSC 115590, $\times 1.5$. 7.19–7.22, *Fluctuaria* cf. *F. undata* (DeFrance, 1826), ventral, anterior, posterior, and lateral views of ventral valve, GSC 115591, $\times 1$. 7.23–7.26, *?Lino-productus* sp.; 7.23–7.25, ventral, posterior, and lateral views of ventral valve, GSC 115592, $\times 1$; 7.26, ventral view of mold of dorsal exterior, GSC 115593, $\times 1$. 7.27, 7.28, *Cancrinella* sp., ventral exterior and mold of dorsal exterior, GSC 115594 and 115595, $\times 2$.

Table 9.—Measurements (in millimeters) of *Liraria paucispina* n. sp. from GSC locality C-5202.

GSC number	Length	Width	Height	Surface length
115589	17.5	17.8+	8.8	27.7
115590	16.9	19.3	7.2	25.6
115587	15.2	17.0	8.7	23.4
115588	12.7	17.7	6.5	20.5

maximum width anterior to hingeline in most specimens; lateral profile strongly convex, most convex in umbonal region; anterior profile and venter almost evenly rounded; trails not produced or differentiated.

Ventral valve strongly inflated posteriorly, most convex in umbonal region; umbo broad; beak small, scarcely overhanging hingeline, with up to three pairs of fine, vertically oriented attachment spines; ears small, flattened, delineated by concave flexures; ornament of fine, rounded costellae, about 11 to 13 per five mm at a surface distance of 15 mm from beak, which increase by intercalation; few rugae limited to sides of umbo and lateral slopes; one or two pairs of prostrate, elongate, laterally or anterolaterally directed spine bases on ears just anterior to hingeline; other spines rare; spines along hingeline usually absent, rarely with one or two pairs of erect spines at hingeline; growth lines very fine, regularly spaced; interior unknown.

Dorsal valve with moderately concave visceral region; prominent rounded protegular node at hingeline; ears small, defined by convex flexures; fine costellae and rugae as in opposite valve; spines not observed, apparently absent; interior unknown.

Measurements.—See Table 9.

Diagnosis.—This species is characterized by modest size, subovate outline, and one pair (rarely two pairs) of elongated, laterally directed, fine spine bases just anterior to the hingeline.

Comments.—*Liraria paucispina*, n. sp., can be differentiated from the type and only other described species, *Liraria lirata* Cooper and Grant, 1975, from the basal Bone Spring Formation (Leonardian–Artinskian) of west Texas, by its modest size, subovate outline, and pair (rarely two pairs) of elongated, laterally directed, fine spine bases near the hingeline.

This species seems to have been attached throughout life normal to its substrate. All observed attachment areas on the ventral beak bear fine, elongated, vertical impressions such as might be made by productid spines. Nearly all of the specimens from GSC locality C-5202 were recovered from a single small lump of limestone crowded with these shells. It is possible that the spat of this species tended to attach to spines of adults of the same species.

Distribution.—GSC locality C-5202 (100+ specimens, mostly ventral valves); GSC locality 56430 (three ventral valves, one dorsal valve mold); GSC locality 56430A (50 ventral valves).

Family Linoproductidae Stehli, 1954
 Subfamily Linoproductinae Stehli, 1954
 Genus *Linoproductus* Chao, 1927
 ?*Linoproductus* sp.
 (Fig. 7.23–7.26)

Description.—Medium size; moderately concavoconvex; outline transversely subovate; maximum width near midlength; ears small, slightly compressed; body cavity estimated to be moderately thick; lateral profile rounded, most convex in umbonal region; anterior profile subtrapezoidal.

Ventral valve strongly inflated posteriorly; umbonal region broad; beak small, not appreciably overhanging hingeline; venter flattened or weakly sulcate; flanks weakly convex, sloping moderately steeply to lateral margins; trail, if present, short; entire surface with fine costellae, about nine to 11 per

five mm near front margin, which increase by intercalation; three to four rugae on sides of umbo; spine bases not observed, probably because of poor preservation; interior unknown.

Dorsal valve moderately concave; ears delineated by weakly convex flexures; rugae strongest near hingeline, one or two of which may extend around visceral disc; ribbing as in opposite valve; spines absent; interior unknown.

Comments.—Poor preservation of the ventral valve and lack of a dorsal interior makes generic identification difficult. In general aspect this species is most similar to *Linoproductus* Chao but this assignment is far from certain.

Distribution.—GSC locality 56430 (two ventral valves; one mold of dorsal valve exterior).

Genus *Fluctuaria* Muir-Wood and Cooper, 1960

Fluctuaria cf. *F. undata* (Defrance, 1826)

(Fig. 7.19–7.22)

1826 *Productus undatus* Defrance, p. 354.

Description.—This description is based on a single, nearly complete ventral valve.

Medium size; strongly convex; outline transversely subovate; greatest width anterior to midlength; lateral profile almost evenly convex; umbonal region most convex, moderately broad; beak small, slightly overhanging hingeline; venter more weakly convex or slightly flattened; flanks moderately spreading, sloping steeply to lateral margins; ears small, defined by slightly concave flexures; entire surface finely costellate with about 11 to 13 costellae per five mm at surface measure of 20 mm from beak; costellae increase by intercalation; entire valve strongly rugose; rugae irregular, sometimes discontinuous, strongest at sides of umbo; spine bases rare on trail, not observed near hingeline because of poor preservation; ventral interior and dorsal valve unknown.

Comments.—This specimen is similar to the broader specimens of *Fluctuaria undata* figured by Koninck (1843:pl. 12, fig. 2; 1847:pl. 5, fig. 3) from the Viséan of Belgium, and Sarycheva (1937:pl. 7, fig. 2a; Sarycheva et al., 1963:pl. 37, fig. 9) from the Serpukhovian of European Russia and the Kuznets.

Distribution.—GSC locality 56430 (one good ventral valve, five questionable ventral valves). A similar form occurs in the Ladrones Limestone of southeastern Alaska.

Subfamily Grandaurispininae Lazarev, 1986

Genus *Cancrinella* Frederiks, 1928

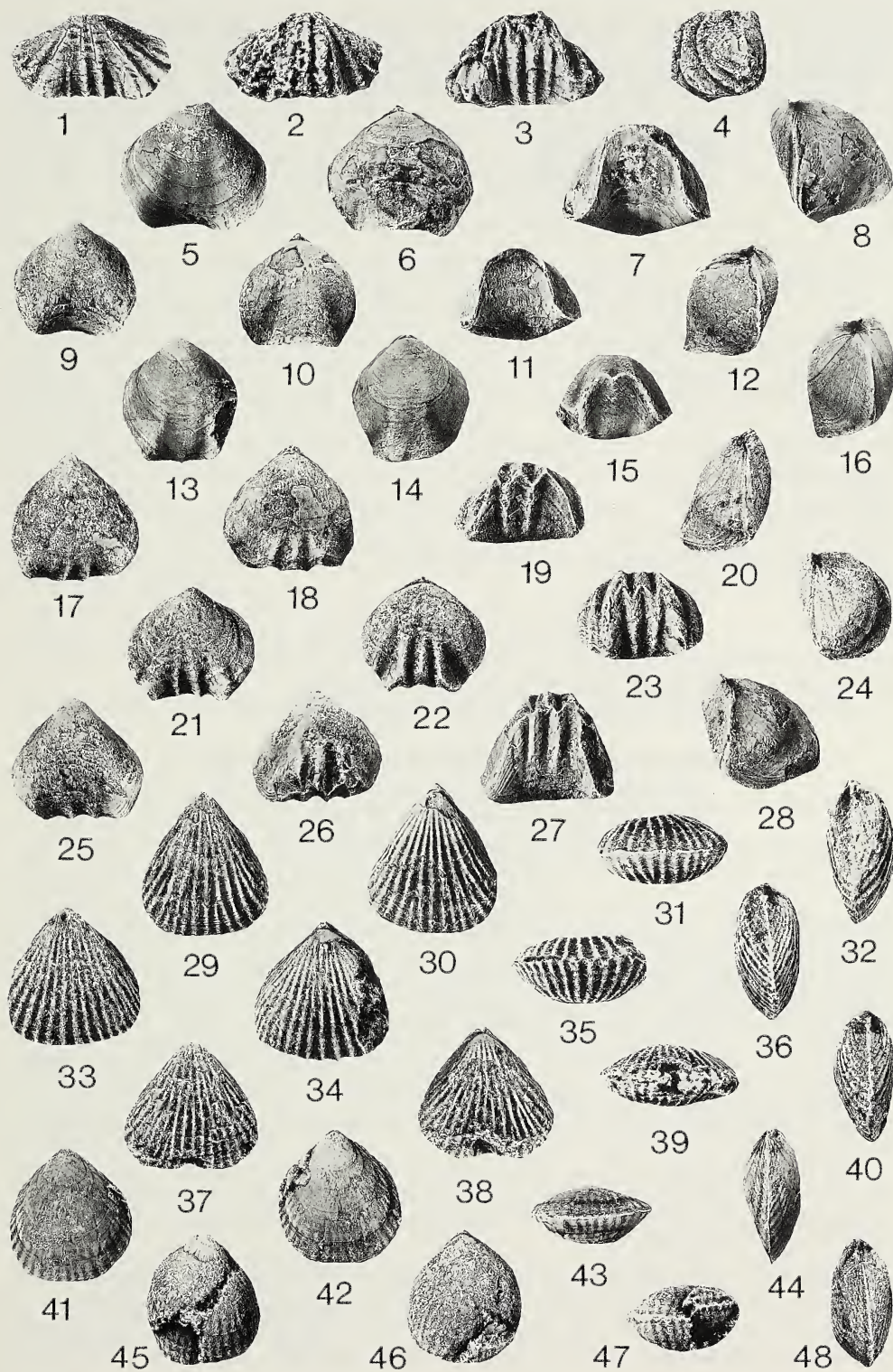
Cancrinella sp.

(Fig. 7.27, 7.28)

Comments.—There are three imperfectly preserved specimens of this genus in the Hare Fiord collections, all from GSC locality 56430. The distinctive fine radial ornament of this species with elongate quincuncially arranged spine bases on

→

Fig. 8.—*Stenoscismatoids* and *rhynchonelloids*. 8.1–8.4, *Stenoscisma* sp., ventral, dorsal, anterior, and lateral views (beak removed by grinding), GSC 115596, $\times 1$. 8.5–8.16, *Careoseptum septentrionalis* n. gen. n. sp., ventral, dorsal, anterior, and lateral views of three specimens, including the holotype (8.9–8.12) and two paratypes, GSC 115597–115599, respectively, $\times 2$. 8.17–8.20, *Cenorhynchia* sp., ventral, dorsal, anterior, and lateral views, GSC 115600, $\times 2$. 8.21–8.28, *Exlaminella insolita* n. gen. n. sp., ventral, dorsal, anterior, and lateral views of two specimens, including the holotype (8.25–8.28, GSC 115601), and the paratype, GSC 115602, $\times 2$. 8.29–8.40, *?Elassonia sverdrupensis* n. sp., ventral, dorsal, anterior, and lateral views of three specimens, including the holotype (8.29–8.32) and two paratypes, GSC 115603–115605, respectively, $\times 2$. 8.41–8.48, *?Hemileurus* sp., ventral, dorsal, anterior, and lateral views of two specimens, GSC 115606 and 115607, $\times 2$.



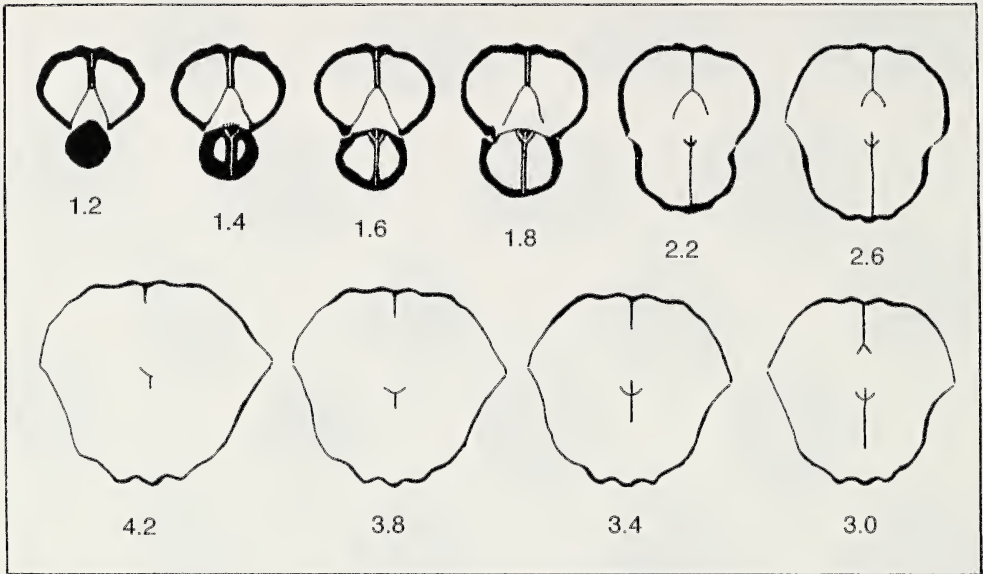


Fig. 9.—Transverse serial sections of *Stenoscisma* sp., GSC 115608, $\times 2.5$. Numbers refer to distance in millimeters from ventral beak.

swollen costellae clearly attest to its generic affinities. However, these few poor, incomplete specimens do not allow specific assignment.

Distribution.—GSC locality 56430 (two ventral valves and one dorsal valve).

Order Pentamerida Schuchert and Cooper, 1931

Superfamily Stenoscismatoidea Oehlert, 1887

Family Stenoscismatidae Oehlert, 1887

Genus *Stenoscisma* Conrad, 1839

Stenoscisma sp.

(Fig. 8.1–8.4, 9)

Description.—This description is based on four specimens, including two complete shells, one ventral valve, and one dorsal valve. One complete specimen was sectioned and is illustrated in Figure 9. The largest complete shell is illustrated in Figure 8. The beak of this weathered specimen was ground down to confirm the presence of a spondylium.

Medium size, moderately to strongly transverse, strongly inequivalved; ventral flanks concave, marked by about three coarse, subangular plicae and possibly a fourth much weaker one; ventral umbonal region smooth; fold and sulcus well developed and marked by two or three strong, angular plicae and up to two much weaker parietal plicae; dorsal valve strongly inflated with convex flanks and ornament complementary to opposite valve.

Ventral interior with deep spondylium elevated well above floor; teeth small, blunt; septum duplex extending anterior to spondylium.

Dorsal interior with short, wide-set sockets; fimbriate cardinal process supported by short, slightly convex hingeplate and long, high median septum; camarophorium narrow, concave, moderately long, extending forward well anterior to dorsally attached portion of septum, with short, low intercamarophoral plate; crura not observed.

Comments.—The few poor specimens of this species do not allow precise identification. We have not been able to find mature individuals of another species of this genus similar in size and proportions to this Canadian species. *Stenoscisma mutabilis* (Chernyshev, 1902) from the Lower Permian of Russia is a highly

variable species, some smaller unusually transverse individuals of which might be generally similar in outline and ornament to this Arctic species.

Distribution.—GSC locality 60194 (three specimens); GSC locality 56430A (one poor ventral valve).

Family Atriboniidae Grant, 1965
Subfamily Psilocamarinae Grant, 1965
Genus *Careoseptum*, new genus

Type Species.—*Careoseptum septentrionalis*, n. sp.

Derivation of Name.—From the Latin *careo*, without or lacking; and *septum*, partition.

Diagnosis.—Small, strongly biconvex; flanks smooth; fold and sulcus rounded, smooth, or with weak median rib; median septa lacking or vestigial in both valves; intercamarophorial plate lacking; hingeplate complete in mature shell, forming septalium with camarophorium.

Comments.—The lack of a dorsal septum makes this genus unique for the superfamily Stenoscismatoidea. The absence of an intercamarophorial plate places it in the family Atriboniidae, subfamily Psilocamarinae. Within this subfamily *Careoseptum* is externally similar only to the genus *Psilocamara* Grant, 1965, described from the Moscovian of Texas and Missouri. Internally, the two genera are greatly different.

Distribution.—Lower Moscovian of Arctic Canada.

Species Assigned.—Known only from the type species.

Careoseptum septentrionalis, new species
(Fig. 8.5–8.16, 10)

Holotype.—Figures 8.9–8.12, GSC 115598, from GSC locality C-5202.

Paratypes.—Figures 8.5–8.8, GSC 115597, from GSC locality 56430; Figures 8.13–8.16, GSC 115599, from GSC locality 56430; Figure 10A, GSC 115609, 10B, GSC 115610.

Description.—Medium size, outline subovate, strongly inequivalved; fold and sulcus absent posteriorly, strongly produced anteriorly, rounded, smooth, or with weak median rib; lateral slopes smooth; stolidium not apparent; shell matter thickened posteriorly.

Ventral valve weakly convex; umbonal region subtending an angle greater than 90 degrees; beak small, subangular, projecting slightly posterior to dorsal valve; foramen small, rounded; delthyrium apparently open; spondylium supported by thick callus posteriorly, free anteriorly; teeth broad, blunt.

Dorsal valve thick, evenly convex on flanks; fold originating in posterior third to half of valve; umbonal region slightly swollen, compressed laterally; septum lacking; camarophorium unsupported except at posterior margin, covered posteriorly; intercamarophorial plate lacking; crura not observed.

Measurements.—See Table 10.

Diagnosis.—Same as for the genus.

Comments.—The authors know of no other species internally similar to *Careoseptum septentrionalis*.

Table 10.—Measurements (in millimeters) of the types of *Careoseptum septentrionalis*, n. sp.

GSC number	Locality	Length	Width	Thickness
115597	56430	10.6	10.7	8.1
115598	C-5202	9.6	9.0	6.4
115599	56430	9.5	8.5	6.5

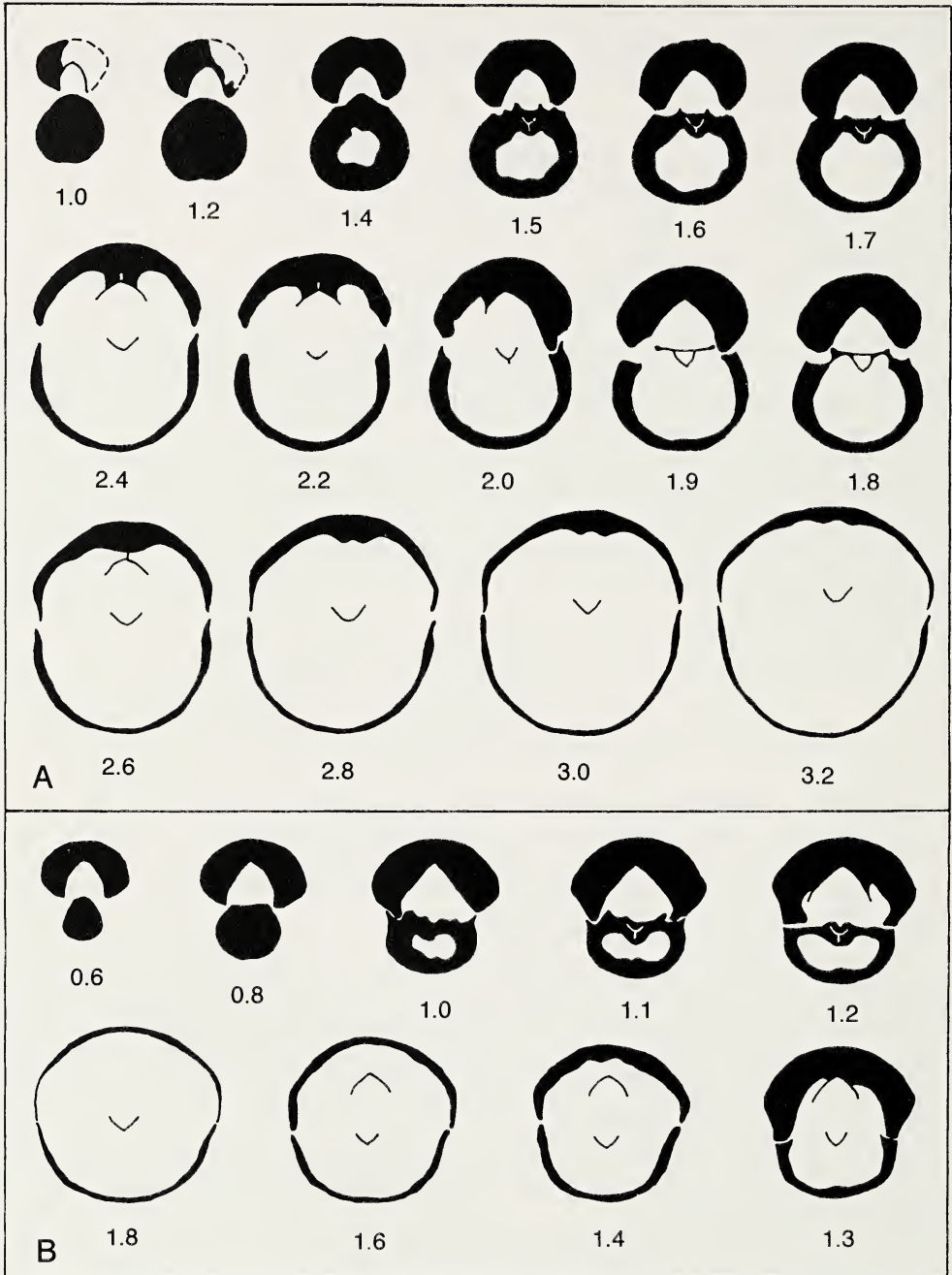


Fig. 10.—Transverse serial sections of *Careoseptum septentrionalis* n. gen. n. sp. Numbers refer to distance in millimeters from ventral beak. A. Large mature specimen, GSC 115609, $\times 4$. B. Small specimen, GSC 115610, $\times 5$.

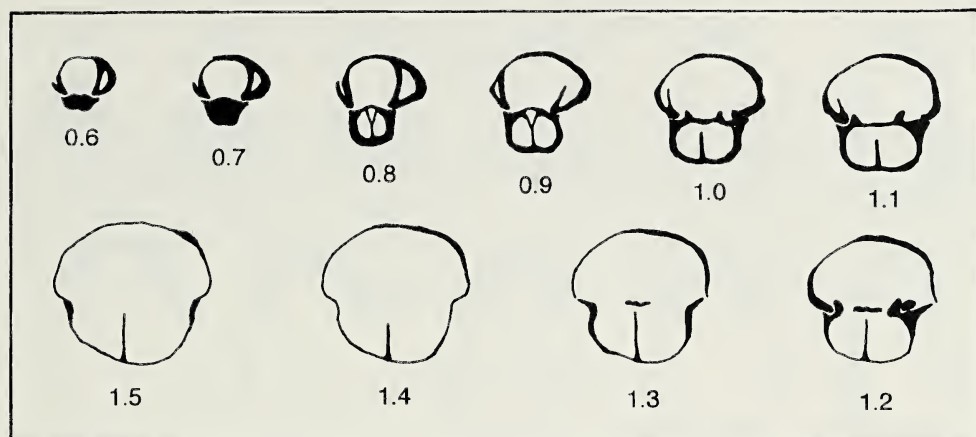


Fig. 11.—Transverse serial sections of *Cenorhynchia* sp., GSC 115611, $\times 5$. Numbers refer to distance in millimeters from ventral beak.

Distribution.—GSC locality 56430 (eight specimens); GSC locality C-5202 (two specimens).

Order Rhynchonellida Kuhn, 1949
 Superfamily Rhynchonelloidea Gray, 1848
 Family Wellerellidae Likharev, 1956
 Genus *Cenorhynchia* Cooper and Grant, 1976
Cenorhynchia sp.
 (Fig. 8.17–8.20, 11)

Description.—Medium size for genus, unequally biconvex; outline rounded subtrigonal, lateral profile subelliptical; anterior or posterior profile subelliptical; umbonal region moderately broad, subtending an umbonal angle of about 90 degrees; fold and sulcus moderately developed and moderately wide; flanks of both valves smooth; fold and sulcus with few strong plicae only in anterior third of valves.

Ventral valve moderately convex in lateral profile; beak slightly incurved, small; deltidial plates not observed; foramen not observed; sulcus originating anterior to midlength; sulcus with two strong, rounded plicae on tongue; interior with stout, short, medially concave dental plates.

Dorsal valve with flattened umbonal region; flanks moderately convex, sloping steeply to lateral margins; fold originating anterior to midlength, rising little above lateral slopes, with three strong, rounded plicae confined to anterior third of valve; interior with complete hingeplate covering short septalium; median septum long, very high, nearly in plane of lateral commissure; sockets wide, defined by high socket ridges; crura not observed.

Comments.—This late Bashkirian or early Moscovian Arctic species is similar in its proportions and ornament to *Cenorhynchia saginata* Cooper and Grant, 1976, and *Cenorhynchia triangulata* Cooper and Grant, 1976, from the Permian of west Texas. It differs from the former in its larger size and complete lack of lateral ribbing. *Cenorhynchia triangulata* is less similar to this Arctic species with its inflated dorsal umbo, obscure lateral ribbing, and laterally compressed ventral beak.

Distribution.—GSC locality 56430 (three specimens, one sectioned).

Genus *Phrenophoria* Cooper and Grant, 1969*?Phrenophoria* sp.

(Fig. 15.20–15.24)

Comments.—A single complete specimen externally similar to the genus *Phrenophoria* Cooper and Grant was not sectioned. Dental plates and a strong dorsal median septum are clearly present which supports this generic assignment but the lack of other internal details prevents certain generic placement. A single disarticulated dorsal valve is nearly identical to that of the complete specimen but adds no additional information concerning morphology.

Distribution.—GSC locality 60194 (two specimens).

Family uncertain

Genus *Exlaminella*, new genus

Type Species.—*Exlaminella insolita*, n. sp.

Derivation of Name.—From the Latin *ex*, without; *lamina*, plate; and *ella*, feminine diminutive.

Diagnosis.—Small, unequally biconvex; outline rounded subtrigonal to subovate; flanks smooth; fold and sulcus with plicae confined to anterior half of valves; interior lacking dental plates or dorsal septum; hingeplate divided, crura falcifer; shell posteriorly thickened in both valves.

Comments.—This genus is unusual in its lack of lateral ribbing and internal plates. The latter feature is found in the Permian genera *Iotina* Cooper and Grant, 1976, and *Ptilotorhynchus* Cooper and Grant, 1976, where the dental plates are fused or suppressed. Both of these genera have strong ribbing on the flanks and much different growth form. *Hemileurus* Cooper and Grant, 1976, also Permian, possesses a similar dorsal interior and ribbing confined to the anterior half of the valves. The ventral interior is conventional with long, slender dental plates. Nevertheless, *Hemileurus* is more likely related to *Exlaminella* than the other Permian genera if growth form, ornament, and dorsal interior are of paramount importance in the phylogeny of this group. In the meantime, we cannot definitely assign this new genus to any known family.

Species Assigned.—Monotypic.

Stratigraphic Range.—Late Bashkirian or early Moscovian of Arctic Canada.

Exlaminella insolita, new species

(Fig. 8.21–8.28, 12)

Holotype.—Figures 8.25–8.28, GSC 115602, from GSC locality 56430.

Paratypes.—Figures 8.21–8.24, GSC 115601, from GSC locality C-5202; Figure 12A, GSC 115612, from GSC locality C-5202; Figure 12B, GSC 115613, from GSC locality C-5202.

Description.—Ventral valve weakly convex; sulcus originating at about midlength, with two strong subangular plicae anteriorly; umbonal region moderately broad, subtending an angle of 90 degrees or more; beak small, slightly incurved; foramen not observed; delthyrium not observed; ventral interior with thick shell matter but with no indication of dental plates.

Dorsal valve moderately convex in umbonal region, sloping steeply to lateral margins; fold originating near or posterior to midlength, rising moderately to high, marked by three short, strong, rounded plicae anteriorly; dorsal interior with thick callus deposits posteriorly; hingeplate divided; crura falcifer, remaining in plane of lateral commissure; low, thick median ridge variably developed.

Measurements.—See Table 11.

Diagnosis.—Same as for genus.

Comments.—Externally this species is similar in size and growth form to the

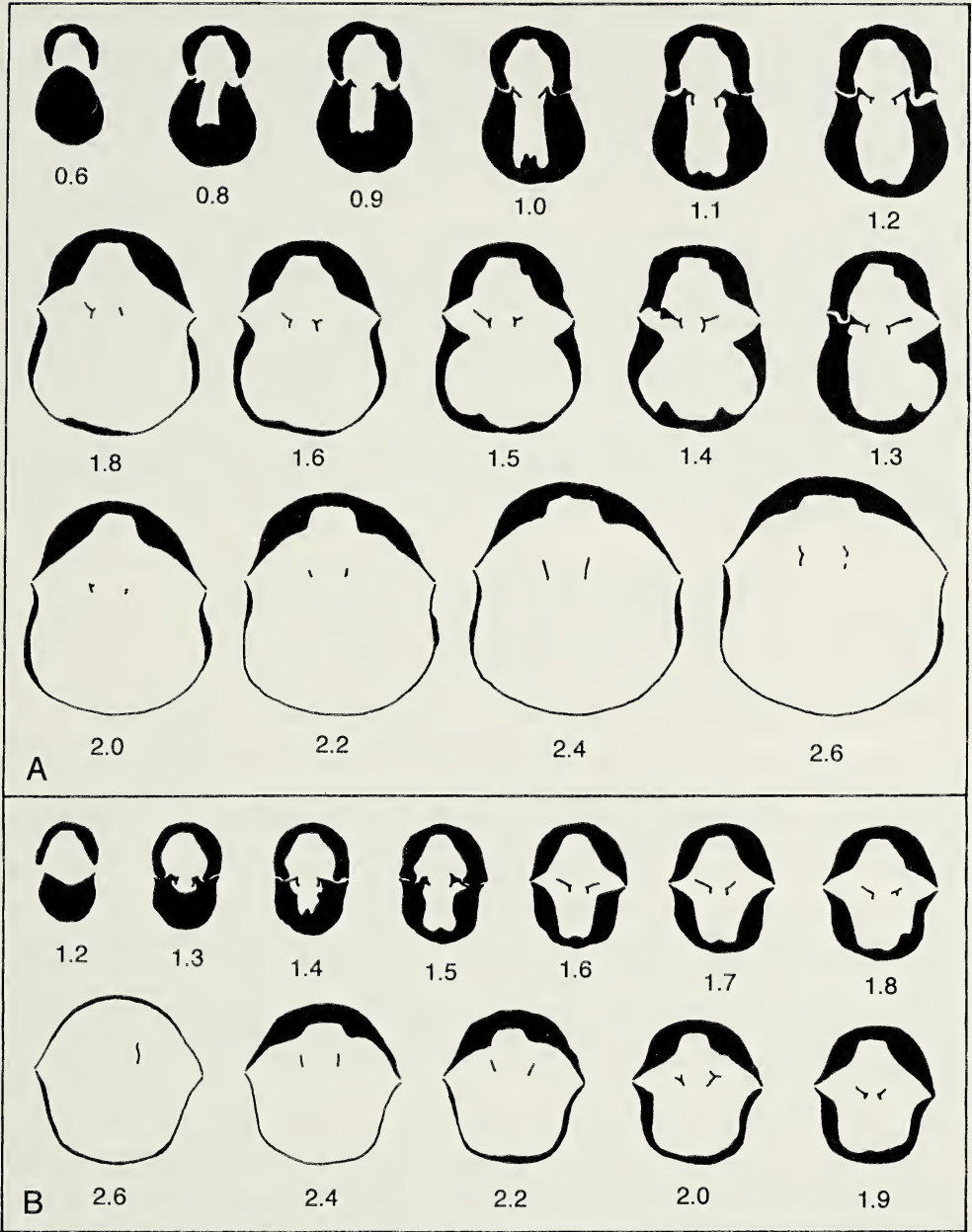


Fig. 12.—Transverse serial sections of *Exlaminella insolita* n. gen. n. sp. Numbers refer to distance in millimeters from ventral beak. A. Large mature paratype, GSC 115612, $\times 4$. B. Juvenile paratype, GSC 115613, $\times 4$.

Table 11.—*Measurements (in millimeters) of Exlaminella insolita, n. gen. n. sp. from the lower Hare Fiord Formation.*

GSC number	Locality	Length	Width	Thickness
115601	C-5202	8.4	9.3	6.5
115602	56430	9.9	9.7	8.0

stenoscismatoid genus *Careoseptum* n. gen. and differs externally only in the possession of the short anterior plicae in the fold and sulcus. *Careoseptum septentrionalis* n. gen. n. sp., the type and only species, may have a weak single plica in the sulcus but never has two as does *Exlaminella insolita*. Internally the two species are very different. *Cenorhynchia* sp. is also externally similar to *Exlaminella insolita* in growth form, size, and ornament. The former differs internally in its high dorsal septum and stout dental plates.

Distribution.—GSC locality 56430 (two specimens); GSC locality C-5202 (three specimens, two sectioned).

Family Petasmatheridae Cooper and Grant, 1976

Genus *Elassonia* Cooper and Grant, 1976

?*Elassonia sverdrupensis*, new species

(Fig. 8.29–8.40, 13)

Holotype.—Figures 8.29–8.32, GSC 115603, from GSC locality 56430.

Paratypes.—Figures 8.33–8.40, GSC 115604, 115605, and 115614, from GSC locality 56430.

Description.—Small, flattened, nearly equally biconvex, outline rounded subtriangular to guttate; lateral and anterior profiles lenticular; fold and sulcus lacking; anterior commissure rectimarginate; both valves completely costate to beaks with numerous bifurcating, intercalating, or simple costae; umbonal regions evenly elongated, usually subtending an angle of less than 90 degrees, margins slightly compressed.

Ventral valve slightly thicker than dorsal valve, weakly and evenly convex in lateral profile; venter weakly convex or flattened; flanks sloping nearly normal to lateral margins, forming subangular beak ridges; beak small, undifferentiated from umbo, suberect; foramen not observed; interior with short, medially concave, thin dental plates.

Dorsal valve more evenly rounded and slightly compressed laterally in umbonal region; dorsum anteriorly flattened or with faint sulcus; otherwise similar in convexity to opposite valve; interior with very short septalium supported by stout, moderately long median septum; hingeplate divided or undivided; crura falcifer, thin, curving ventrad.

Measurements.—See Table 12.

Diagnosis.—This species can be differentiated by small size, thin profile, triangular outline, the lack of a fold and sulcus, and bifurcating costae.

Comments.—These specimens, lacking a fold and sulcus, resemble juvenile specimens of much larger species. However, we are convinced that these 14 specimens are mature individuals because of the uniformity in size of the specimens.

Assignment of this unusual species to the Permian genus *Elassonia* Cooper and Grant is arbitrary. We have little doubt that it represents an undescribed genus but the indifferent preservation of this collection and lack of pristine specimens inhibits us from proposing one.

Distribution.—GSC locality 56430 (14 specimens, eight complete or nearly complete, two sectioned).

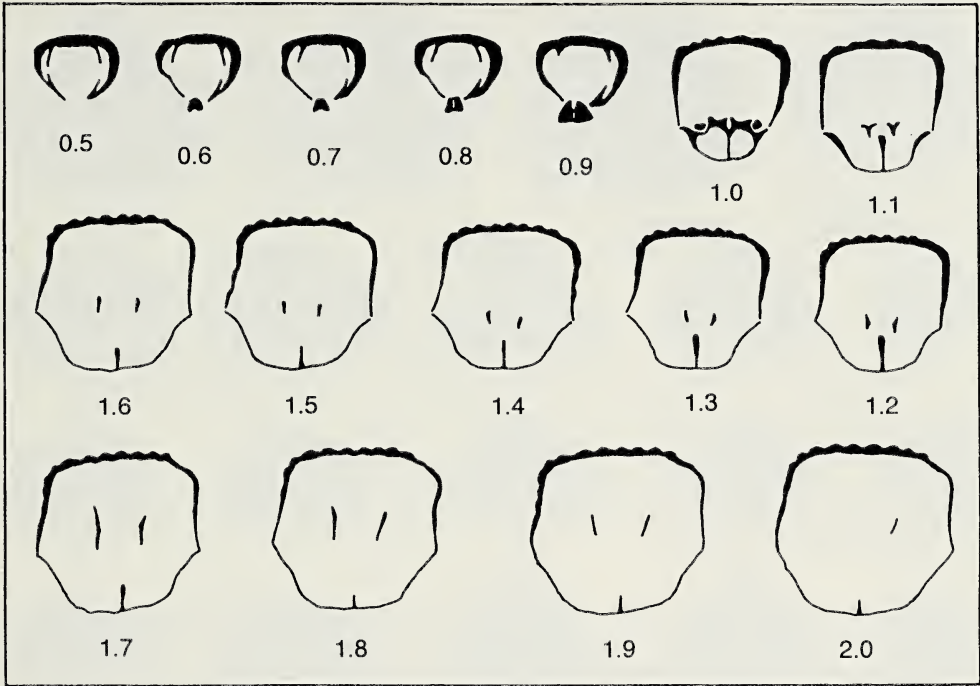


Fig. 13.—Transverse serial sections of *?Ellassonia sverdrupensis* n. sp., paratype, GSC 115614, $\times 5$. Numbers refer to distance in millimeters from ventral beak.

Family Allorhynchidae Cooper and Grant, 1976
Genus *Hemileurus* Cooper and Grant, 1976
?Hemileurus sp.
(Fig. 8.41–8.48, 14)

Description.—Small, almost equally biconvex, outline longitudinally subovate; lateral and anterior profiles thinly lenticular; fold and sulcus lacking; anterior commissure rectimarginate; umbonal regions smooth, anterolateral margins with weak costellae; beak ridges rounded.

Ventral valve slightly thicker than dorsal valve, evenly convex; umbonal region slightly extended, subtending an angle of about 90 degrees; beak small, nearly straight, inconspicuous; posterolateral margins slightly compressed in some specimens; interior with short, thin, straight dental plates; muscle field deeply incised.

Dorsal valve evenly convex, with slightly flattened dorsum anteriorly; umbonal region slightly swollen, weakly compressed laterally; interior with divided hingeplate; median septum lacking; crura falcifer, not rising but remaining in plane of lateral commissure.

Comments.—These small specimens, lacking any indication of a fold and sulcus, are probably juveniles of the genus *Hemileurus* Cooper and Grant, agreeing

Table 12.—Measurements (in millimeters) of *?Ellassonia sverdrupensis*, n. sp. from GSC locality 56430 of the lower Hare Fiord Formation.

GSC number	Length	Width	Thickness
115603	10.5	9.5	5.3
115604	10.1	9.8	5.0
115605	9.5	9.9	4.4

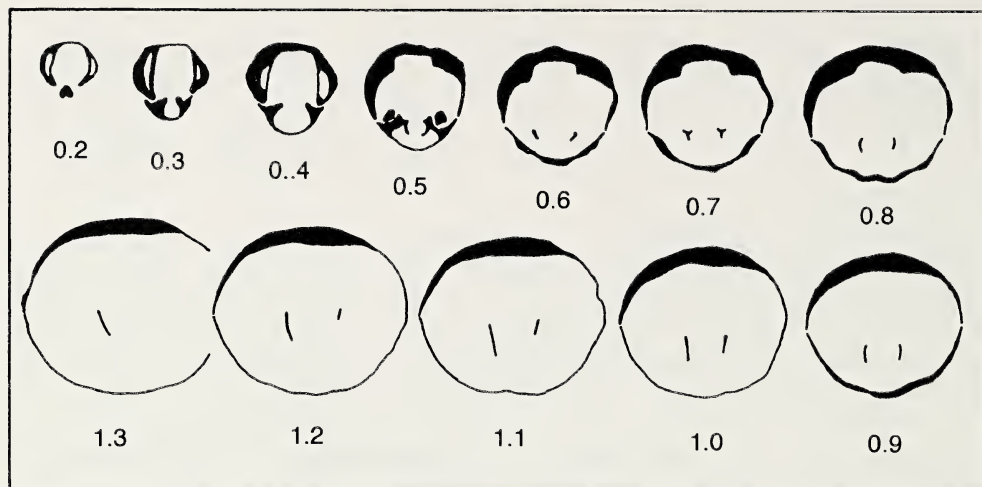


Fig. 14.—Transverse serial sections of *Hemileurus* sp., GSC 115615, $\times 8$. Numbers refer to distance in millimeters from ventral beak.

in most respects with the type species of that genus, except for their lack of a fold and sulcus and having more numerous costellae near the margins. They are not similar to any other species from the Hare Fiord Formation.

Distribution.—GSC locality 56430 (five specimens, one sectioned).

Family Tetracameridae Likharev, 1958

Genus *Septacamera* Stepanov, 1937

Septacamera sp.

(Fig. 15.1–15.4)

Description.—This description is based on a single, nearly complete specimen.

Medium size for genus, strongly inequivalved; outline and lateral profile rounded subtriangular, anterior profile subquadrate; anterior surface flattened; anterior commissure uniplicate with large ventral tongue; fold and sulcus moderately well developed, originating in umbonal region of both valves; plicae simple, subangular, numbering three in sulcus, four on fold, and five or six on each lateral slope, lateral two or three very weak.

Ventral valve gently convex with sharply geniculated tongue in sulcus; beak and foramen not preserved.

Dorsal valve thick, strongly inflated with weakly convex dorsum; lateral slopes bent sharply ventrad with flattened sides.

Interior not observed.

Comments.—This species is similar in size, lateral profile, and ornament to *Septacamera kutorgae* (Chernyshev, 1902) from the Lower Permian of Russia. It differs in having a more triangular outline, a more quadrate anterior profile, and a flatter fold.

Distribution.—GSC locality 60194 (one specimen).

Family Pontisiidae Cooper and Grant, 1976

Genus *Antronaria* Cooper and Grant, 1976

Antronaria annosa, new species

(Fig. 15.5–15.19, 16)

Holotype.—Figures 15.5–15.9, GSC 115617, from GSC locality 56430.

Paratypes.—Figures 15.10–15.14, GSC 115618, from GSC locality 56430; Figures 15.15–15.19 and 16, GSC 115619, from GSC locality 60194.

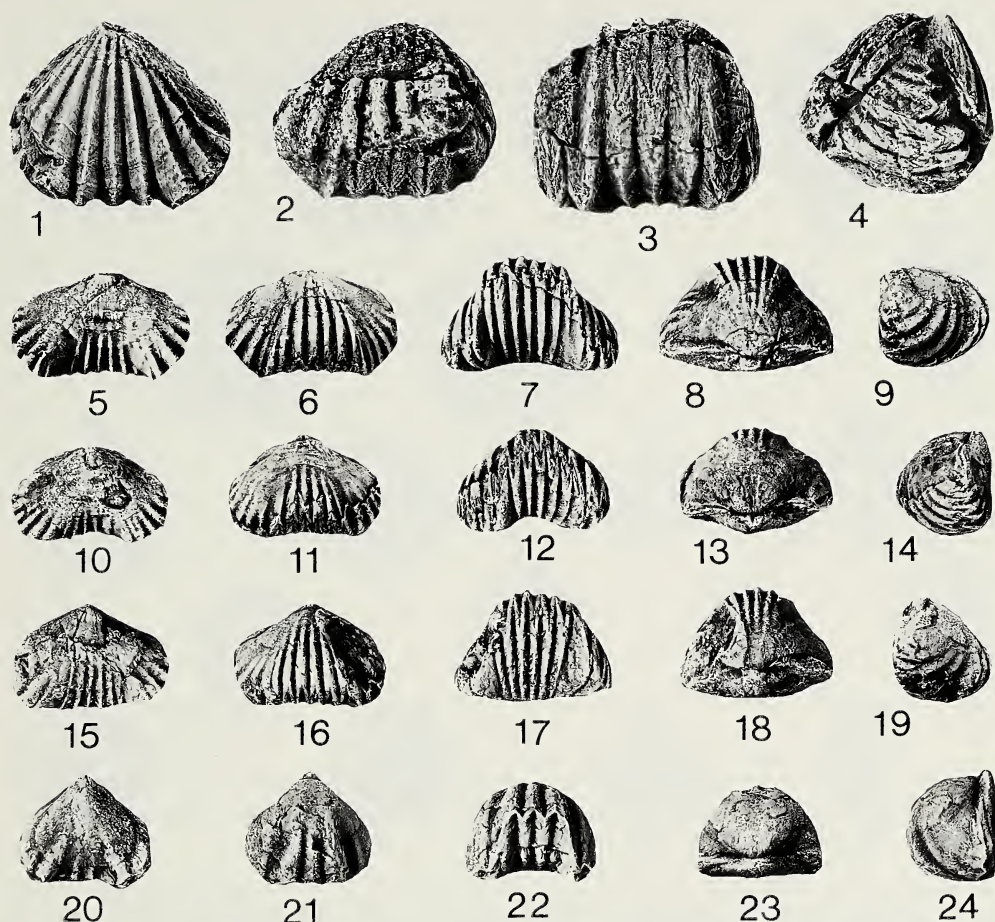


Fig. 15.—Rhynchonelloids. 15.1–15.4, *Septacamera* sp., ventral, dorsal, anterior, and lateral views, GSC 115616, $\times 1$. 15.5–15.19, *Antronaria annosa* n. sp., ventral, dorsal, anterior, posterior, and lateral views of three specimens, including the holotype (15.5–15.9), GSC 115617–115619, respectively, $\times 1$. 15.20–15.24, *?Phrenophoria* sp., ventral, dorsal, anterior, posterior, and lateral views, GSC 115620, $\times 1$.

Description.—Larger than average for genus, unequally biconvex; outline subelliptical; umbonal region very broad, subtending an angle of 135 degrees or more; both valve margins near posterior commissure compressed; fold and sulcus wide, well developed, originating in posterior half or third of valves; anterior commissure strongly uniplicate; beak short, inconspicuous, scarcely extending posterior to opposite valve; deltidial plates not observed; umbonal regions smooth, remainder of valves costate; flanks with five to seven subangular costae, originating well anterior to umbonal region; fold and sulcus with five to seven subangular costae.

Ventral valve weakly to moderately convex or flattened in lateral profile, flat or concave in anterior profile; umbonal region slightly swollen, flanks flattened or weakly concave; sulcus originating posterior to midvalve, in anterior portion of umbonal region; sulcus rounded, evenly curving dorsad, not geniculate; dental plates strong, diverging anteriorly, of moderate length.

Dorsal valve rounded subtrigonal in lateral profile, strongly convex in anterior profile; umbonal region laterally defined by concave flexures; flanks convex, curving steeply to lateral margins; fold originating near midlength, well defined and elevated anteriorly, flattened or weakly convex in anterior profile; costae on fold not depressed as in type species; interior with flattened, complete hingeplate;

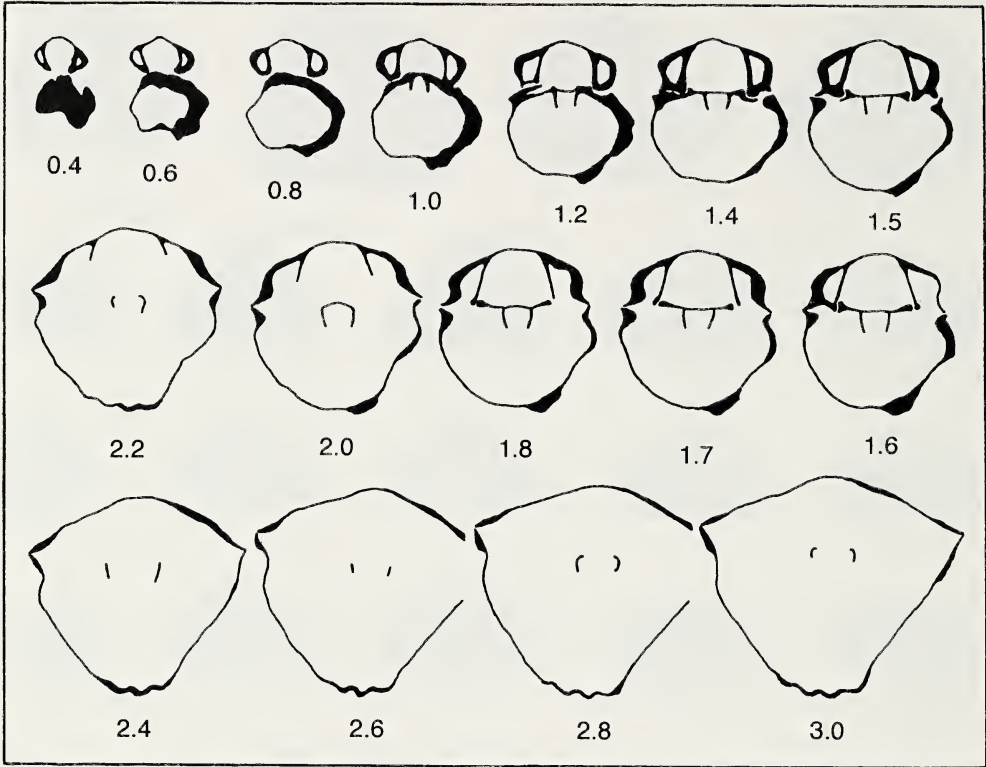


Fig. 16.—Transverse serial sections of *Antronaria annosa* n. sp., paratype GSC 115619, $\times 2.5$. Numbers refer to distance in millimeters from ventral beak.

crural bases attached to dorsal surface of hingeplate, slightly convergent, extending forward in plane of commissure as long, slender, medially concave crura.

Measurements.—See Table 13.

Diagnosis.—This species is characterized by evenly rounded lateral margins, inconspicuous ventral beak, smooth umbonal regions, and lack of depressed costae on the fold.

Comments.—These specimens are similar to those illustrated by Cooper and Grant (1976) of *Antronaria transversa* (King) from the Wolfcampian of Texas. They differ in minor details, having more evenly rounded lateral margins, a smaller ventral beak, the ribbing originates more anteriorly, and they lack depressed medial ribs on the fold.

This Arctic species is the first reported in the literature from strata older than the early Permian.

Table 13.—*Measurements (in millimeters) of Antronaria annosa n. sp. (King).*

GSC number	Locality	Length	Width	Thickness
115617	56430	16.2	23.5	14.9
115618	56430	14.4	20.6	13.2
115619	60194	15.5	20.8	13.7



Fig. 17.—Athyridoids. 17.1–17.8, *Camarium nuperum* n. sp., ventral, dorsal, anterior, and lateral views of two specimens, including the holotype (17.5–17.8), GSC 115621 and 115622, $\times 3$. 17.9–17.20, *Nucleospira aquilonaris* n. sp., ventral, dorsal, anterior, and lateral views of three specimens, including the holotype (17.9–17.12), GSC 115623–115625, respectively, $\times 2$.

Distribution.—GSC locality 56430 (four specimens); GSC locality 60194 (two specimens, one sectioned).

Order Athyridida Boucot, Johnson, and Staton, 1965
 Suborder Athyridina Boucot, Johnson, and Staton, 1965
 Superfamily Athyridoidea Davidson, 1881
 Family Meristellidae Waagen, 1883
 Subfamily Meristinae Hall and Clarke, 1895
 Genus *Camarium* Hall, 1859
Camarium nuperum, **new species**
 (Fig. 17.1–17.8, 18)

Holotype.—Figures 17.5–17.8, GSC 115621, from GSC locality 56430.

Paratypes.—Figures 17.1–17.4, GSC 115622, from GSC locality 564530; Figure 18, GSC 115626, from GSC locality 56430.

Description.—Small, subequally biconvex, outline subovate; maximum width attained near mid-length; lateral and anterior profiles lenticular; fold lacking but shallow sulcus present on anterior half

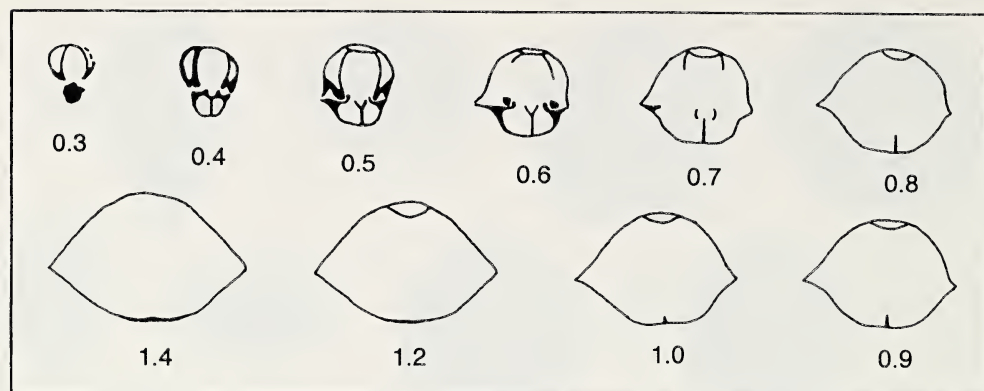


Fig. 18.—Transverse serial sections of *Camarium nuperum* n. sp., GSC 115626, $\times 6$. Numbers refer to distance in millimeters from ventral beak.

of ventral valve producing slight emargination; posterolateral margins slightly compressed; anterior commissure nearly rectimarginate with slight medial dorsal flexure; surfaces smooth except for fine growth lines.

Ventral valve with slightly swollen umbonal region with moderately broad posterolateral extremities which subtend an angle greater than 90 degrees; beak small, incurved; foramen not observed; venter and lateral slopes evenly and moderately convex; sulcus originating near midlength, becoming moderately deep and rounded near anterior margin; interior with medially concave dental plates and low, short, convex shoelifter process which originates in umbonal region; teeth broad, blunt.

Dorsal valve with sides of umbonal region slightly compressed, flanks and dorsum evenly convex near midvalve, dorsum slightly flattened anteriorly; interior with septalium supported by high median septum which extends forward nearly as far as shoelifter process in opposite valve; crura and spiralia not observed.

Measurements.—See Table 14.

Diagnosis.—This species can be differentiated by its small size and distinct ventral sulcus.

Comments.—Amsden (1968) validated the genus *Camarium* Hall after discovering that it lacks mystrochial plates, unlike the genus *Merista* Suess which has them. The type species of *Camarium*, *C. typa* Hall, is from the Upper Silurian of the eastern United States. Carter (1967) described an anachronistic species of *Camarium* as *Merista maccullochensis* from the Lower Mississippian of Texas. Campbell and Engel (1963) also reported *Merista* sp. in the Tournaisian of New South Wales. All other reports of *Camarium* are from Middle Devonian or older strata.

Camarium nuperum n. sp. is similar to the above-mentioned species of Tournaisian age, differing only in the presence of a distinct ventral sulcus.

Distribution.—GSC locality 56430 (four specimens, one sectioned).

Table 14.—*Measurements (in millimeters) of the types of Camarium nuperum, n. sp., from GSC locality 56430.*

GSC number	Length	Width	Thickness
115621	9.4+	9.0	6.1
115622	8.2	8.1	4.9

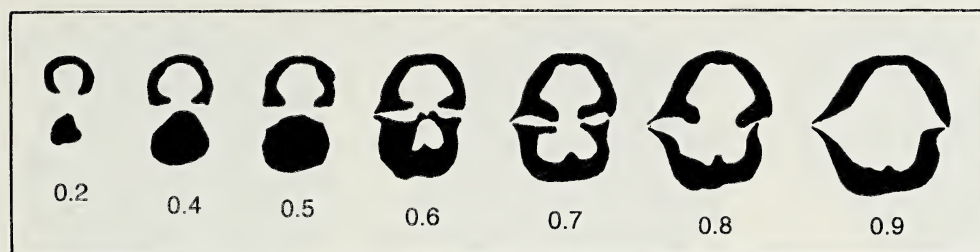


Fig. 19.—Transverse serial sections of *Nucleospira aquilonaris* n. sp., GSC 115627, $\times 5$. Numbers refer to distance in millimeters from ventral beak.

Family Nucleospiridae Davidson, 1881

Genus *Nucleospira* Hall, 1859

Nucleospira aquilonaris, new species

(Fig. 17.9–17.20, 19)

Holotype.—Figures 17.9–17.12, GSC 115623, from GSC locality 56430.

Paratypes.—Figures 17.13–17.20, two shells, GSC 115624 and 115625, from GSC locality 56430; Figure 19, GSC 115627, from GSC locality 56430.

Description.—Small, subequally and moderately biconvex; outline subovate to weakly subpentagonal; greatest width near midlength; anterior margin rounded to slightly emarginate; lateral and anterior profiles lenticular; surfaces smooth except for irregularly spaced growth varices; micro-ornament not preserved; fold lacking; sulcus lacking or weak, shallow sulcus present on some ventral valves; anterior commissure rectimarginate to weakly uniplicate; shell substance very thick.

Ventral valve moderately inflated, evenly convex in lateral profile; umbonal region broad, slightly compressed at margins; beak small, acute, straight, projecting slightly posterior to opposite valve; foramen triangular; interarea acutely triangular, flattened to weakly concave; sulcus, if present, shallow, weak, originating in anterior half of valve; interior with large, blunt, unsupported teeth and low, weak median ridge.

Dorsal valve with slightly swollen umbonal region defined laterally by concave flexures and compressed lateral margins; dorsum evenly convex or slightly flattened anteriorly; dorsal interarea not detected; interior with high bilobed hingeplate and thick myophragm; other details not observed.

Measurements.—See Table 15.

Diagnosis.—This species is characterized by its thickened shell, well-developed ventral beak, flattened dorsum, and moderately inflated lateral profile.

Comments.—Upper Carboniferous *Nucleospira* are very rare. *Nucleospira superata* Easton, 1962, from the Cameron Creek Formation (Lower Morrowan) of Montana, is the only other Upper Carboniferous species we can find in the literature and is of very early Late Carboniferous age, much older than the Hare Fiord species. The latter is more transverse than *N. aquilonaris*, with an inconspicuous ventral beak, and the lateral slopes are more flattened in anterior profile.

Brunton (1984) also failed to find other evidence of Upper Carboniferous species of this genus. Cooper and Grant (1976) state that it generally had been

Table 15.—Measurements (in millimeters) of *Nucleospira aquilonaris*, n. sp., from GSC locality 56430.

GSC number	Length	Width	Thickness
115623	9.7	9.9	6.6
115624	9.6	8.7	6.3
115625	8.5	8.6	5.8

believed that *Nucleospira* became extinct at the end of the Early Carboniferous but they described a typical species, *N. cunctata*, from the Lower Permian of west Texas. The reduced ventral median ridge found in *N. aquilonaris* is also seen in this Permian species.

Distribution.—GSC locality 56430 (40 specimens, two sectioned).

Order Spiriferida Waagen, 1883
Suborder Spiriferidina Waagen, 1883
Superfamily Ambocoelioidea George, 1931
Family Ambocoeliidae George, 1931
Genus *Crurithyris* George, 1931
Crurithyris cf. *tschernyschewi* Likharev, 1939
(Fig. 20.18–20.21)

1902 *Ambocoelia planoconvexa* Shumard: Chernyshev, p. 196, pl. 20, fig. 1; pl. 49, fig. 7.

1939 *Ambocoelia* (*Crurithyris*) *tschernyschewi* Likharev, p. 108, pl. 27, fig. 5.

Description.—Hingeline somewhat shorter than width; ventral valve moderately convex; greatest thickness at or just posterior to hingeline; ventral umbo narrow and weakly incurved, beak not overhanging hinge plane; area low and concave under beak, clearly restricted, triangular; ventral sinus absent but valve flattened along midline; dorsal valve almost flat or slightly convex with shallow groove anteriorly; area low, triangular, well delimited; surface smooth, with few irregular coarse growth varices anteriorly; dental adminicula in ventral valve absent; other internal features not observed.

Diagnosis.—A small, transversely ovate *Crurithyris* with greatest width no more than ten mm.

Comments.—The general shape, size, and characters of the ventral valve allow us to conclude that this species is very close to or identical with *Crurithyris tschernyschewi* Likharev. However, our restricted material, consisting of only one complete shell and one ventral valve, are both poorly preserved and compel us to avoid a certain definition. The other nearest known species to ours is *Crurithyris expansa* Dunbar and Condra, 1932, from the Wabaunsee Group (Permian) in Nebraska. This species differs in its much more incurved ventral umbo with the apex lying approximately in the plane of the dorsal valve. *Crurithyris planoconvexa* (Shumard, 1855), from the Pennsylvanian and Lower Permian of North America and Europe, differs in its much more convex ventral valve with more stout, incurved ventral umbo and much smaller size.

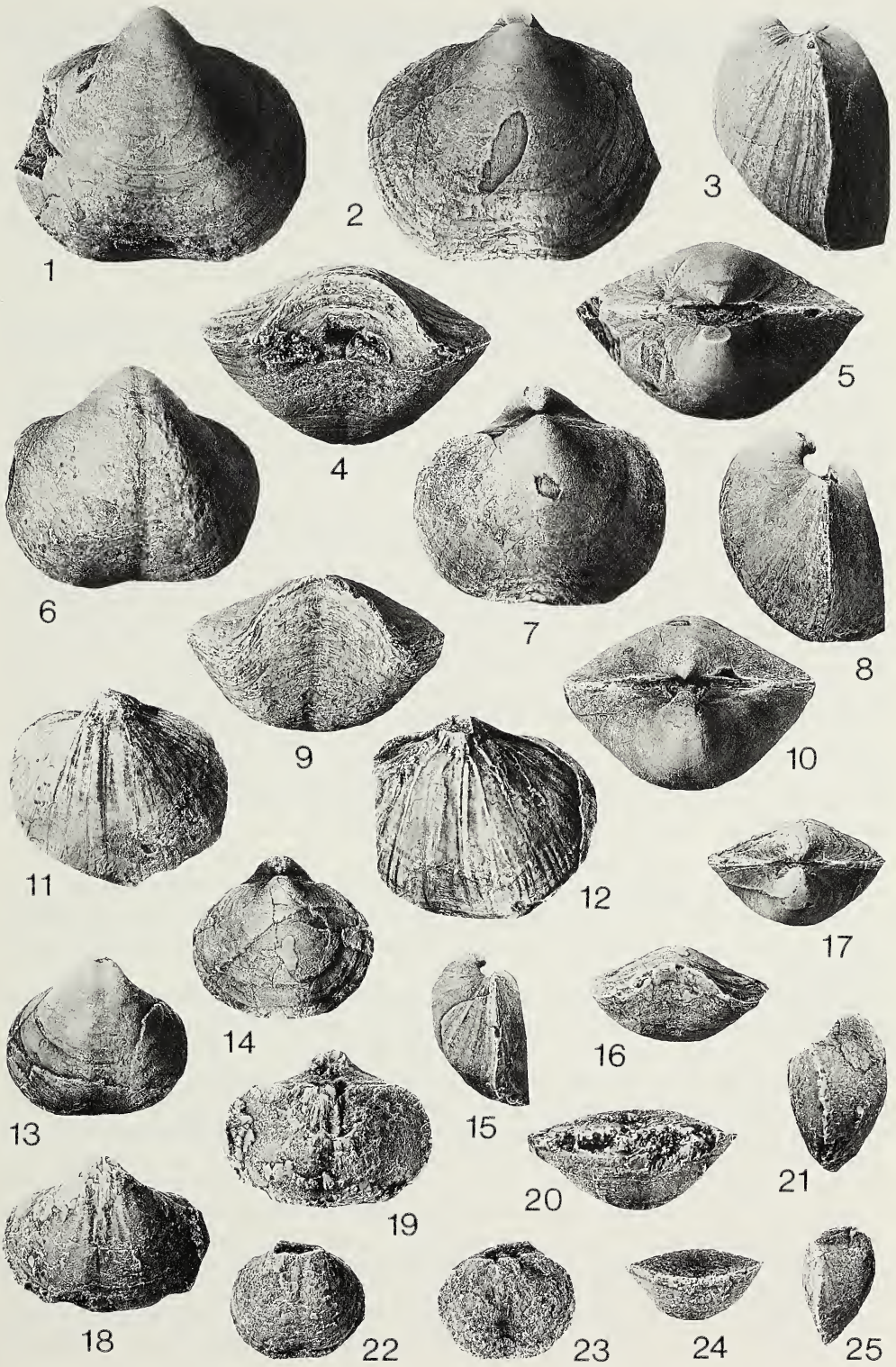
Distribution.—Both specimens are from GSC locality 56430.

Crurithyris sp.
(Fig. 20.22–20.25)

Comments.—A second species of *Crurithyris* was found at GSC locality 56430. This one is characterized by its small size, more rounded outline, more tumid ventral valve, and more flattened dorsal valve than the previously described spe-

→

Fig. 20.—Ambocoelioids and martinioids. 20.1–20.17, *Tirannia walteri* n. sp.; 20.1–20.10, 20.13–20.17, ventral, dorsal, lateral, anterior, and posterior views of three specimens, including the holotype (20.1–20.5), GSC 115628–115630, respectively; 20.11, 20.12, ventral molds showing vascular marks, GSC 115631 and 115632; all $\times 1$. 20.18–20.21, *Crurithyris* cf. *C. tschernyschewi* Likharev, 1939, ventral, dorsal, anterior, and lateral views of a spalled shell, GSC 115633, $\times 3$. 20.22–20.25, *Crurithyris* sp., ventral, dorsal, anterior, and lateral views, GSC 115634, $\times 3$.



cies. Precise identification of this species is impossible because of the paucity of specimens, only two shells, one with a broken ventral beak.

Superfamily Martinioidea Waagen, 1883
Family Martiniidae Waagen, 1883
Subfamily Martininae Waagen, 1883
Genus *Tiramnia* Grunt, 1977
Tiramnia walteri, new species
(Fig. 20.1–20.17)

Holotype.—GSC 115628, Figures 20.1–20.5, GSC locality 56430.

Paratypes.—GSC 115629 and 115630, Figures 20.6–20.10, 20.13–20.17, same collection as the holotype; GSC 115631 and 115632, Figures 20.11 and 20.12, vascular impressions of two ventral valves; all from GSC locality 56430.

Description.—Medium to large for genus, ventribiconvex, usually wider than long; outline transversely oval to subpentagonal, greatest width attained near or anterior to midlength; ventral valve one and one-half times thicker than dorsal valve; anterior commissure uniplicate; fold and sulcus wide, shallow, and poorly delimited, developed only anteriorly; ornamentation lacking and surface smooth except for growth lines and irregularly spaced growth varices; spalled surfaces may show faint radial striations in front part of some adult specimens.

Ventral valve most convex in umbonal region; beak small, incurved; umbonal region moderately broad, only moderately extended posterior to hingeline; flanks gently convex; sulcus originates obscurely some distance in front of beak as narrow, weak furrow becoming wider and somewhat deeper past midway to front margin, where in some shells its sides slope gently toward faint depression along midline; some variation in shape of sulcus; often furrow is almost obscure and sulcus depression is very softly curved, producing moderate tongue at anterior commissure; hingeline usually little less than half width of shell; ventral interarea small, triangular, moderately high and curved, often obscurely defined, with apical angle of about 115 to 120 degrees; delthyrium open.

Ventral muscle field narrow, fusiform, deeply impressed, located mostly within umbonal region; posterior part of adult valves thickened; vascular impressions distinct, radial, bifurcating anteriorly.

Dorsal valve transversely subovate in outline, slightly thinner than opposite one, with moderately gibbous umbonal region and inconspicuous beak; fold arises obscurely in anterior part of valve and rises to its maximum height at front margin, where it is obscurely delimited; dorsal interarea orthocline, less than one-third height of ventral, with broad, open notothyrium; muscle scars very simple, radially dissected and lightly impressed; other internal details not observed.

Measurements.—See Table 16.

Diagnosis.—This species is characterized by comparatively large size (as much as 40 mm long and 50 mm wide), transversely subovate to subpentagonal outline, longer thicker ventral valve than dorsal, and fold and sulcus only clearly expressed anteriorly.

Comments.—*Tiramnia walteri* n. sp. is similar in general outline to *Martinia? triquetra* Gemmellaro, 1899, sensu Grunt and Dmitriev, 1973, from the Nizhneganskaya Subsuite, Murgabian Stage, lower part of the Upper Permian of the southeastern Pamir Mountains. The latter differs from *Tiramnia walteri* n. sp. in having a much longer hingeline and a deeper, more distinctly acute sulcus.

Tiramnia greenlandica Dunbar, 1955, from the Permian Martiniakalk of east

Table 16.—*Measurements (in millimeters) of Tiramnia walteri, n. sp. from GSC locality 56430.*

GSC number	Length	Width	Thickness	Hingeline
115628	39.5	43.7	26.5	17.1
115629	35.4	37.5	23.8	23.2
115630	24.7	26.8	14.7	10.4

Greenland, is very similar to young specimens of this new species. Mature forms of *T. walteri* n. sp. differ in being much larger, they mostly have a less stout umbo and a shorter and less curved beak; the sulcus is more obscure posteriorly and lacks angular borders anteriorly.

Distribution.—*Tiramnia walteri* n. sp. is abundant at GSC localities 56430 (37 specimens) and C-4011 (22 specimens). It also occurs at GSC localities 56430A (seven specimens) and C-4084 (seven specimens). A similar or identical species occurs in the Ladrões Limestone of southeastern Alaska.

***Tiramnia grunti*, new species**
(Fig. 21.1–21.16)

v.1977 *Tiramnia semiglobosa* Chernyshev, 1902:Grunt, p. 66, pl. 11, fig. 8, 9.

v.1977 *Tiramnia greenlandica* Dunbar, 1955:Grunt, p. 64, pl. 11, fig. 4, 6, non 5.

Holotype.—GSC 115635, Figures 21.1–21.5, from GSC locality 56430.

Paratypes.—GSC 115636–115638, Figures 21.6–21.16, all from GSC locality 56430.

Description.—Small to medium size for genus, moderately to strongly subequally biconvex; outline longitudinally subovate to almost round with dorsal valve often almost same length as opposite valve; hingeline much less than greatest width, often one-third or less; maximum width attained near midlength; fold and sulcus obscure posteriorly and weak or moderately developed anteriorly, where they produce weakly or clearly uniplicate commissure; shell substance very thin; surface almost smooth, rarely with a few visible growth varices near anterior commissure.

Ventral valve moderately to considerably inflated, rounded in outline, with greatest thickness near midlength; umbo short and suppressed; small beak, not extending posteriorly to hingeline; interarea low, catacline, concave, poorly differentiated from flanks; delthyrium wide, forming equilateral triangle and occupying approximately one-half of interarea; deltidial plates narrow; sulcus obscure, shallow, appearing near midlength; some specimens with narrow furrow along midline, which begins on umbo and extends to end of moderately long tongue; ventral interior with narrow, deeply impressed fusiform muscle field surrounded by radial vascular impressions; most prominent vascular impression lies on midline and continues to midlength.

Dorsal valve usually as inflated as opposite valve; outline rounded or subpentagonal with large, slightly tumid umbonal region and small beak protruding posteriorly; dorsal interarea low, narrowly triangular, orthocline with open nothothyrium; fold absent or weakly expressed near anterior margin; interior with delicate cardinalia; muscle scars weakly impressed.

Measurements.—See Table 17.

Diagnosis.—This species is characterized by its comparatively small size, rounded outline, almost equidimensional ventral and dorsal valves, prominent dorsal umbo, very weak fold, and moderate or weak sulcus.

Comments.—*Tiramnia grunti* n. sp. varies in such important characteristics as relative length of the dorsal and ventral valves, depth of sulcus, and thickness. Some specimens show extreme variation in one or more of these characters but are united by a multitude of intermediate forms.

Tiramnia grunti n. sp. is most similar to *Martinia? corculum* Kutorga, 1842, from the early Permian (Asselian?) near Sterlitamak, Bashkiria, south Urals. The latter differs in being smaller and having a flatter and shorter dorsal valve with an obscure umbo. *Tiramnia greenlandica* (Dunbar, 1955), from the Permian Martiniakalk of east Greenland, differs also in its wider, more subtriangular outline and wider sulcus with rather angular borders.

Distribution.—This is the most numerous species at GSC locality 56430 (144 good specimens plus several hundred disarticulated valves). Six specimens were found at GSC locality 56430A. It is known also, but not described, from the Upper Carboniferous of Cape Chaika, Ugor Peninsula, northern Ural Mountains, Russia, and the Ladrões Limestone of southeastern Alaska.

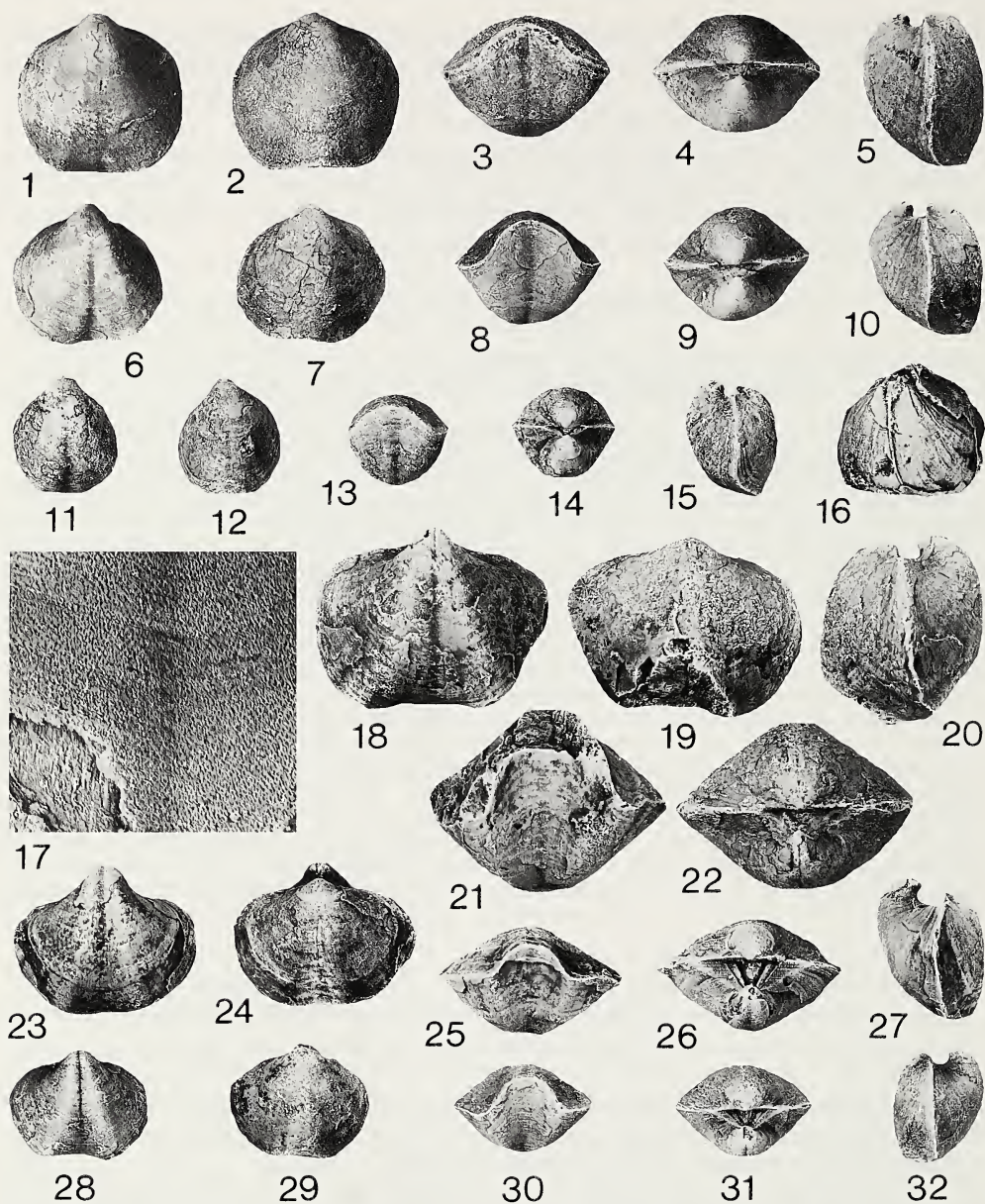


Fig. 21.—Martinioids. 21.1–21.16, *Tiramnia grunti* n. sp.; 21.1–21.15, ventral, dorsal, anterior, posterior, and lateral views of three specimens, including the holotype (21.1–21.5), GSC 115635–115637, respectively; 21.16, mold of ventral interior showing vascular marks, GSC 115638, $\times 1$. 21.17–21.32, *?Heteraria canadiensis* n. sp.; 21.17, micro-ornament, GSC 115639, $\times 10$; 21.18–21.32, ventral, dorsal, lateral, anterior, and posterior views of three specimens, including the holotype (21.18–21.22), GSC 115640–115642, respectively, $\times 1.5$.

Table 17.—Measurements (in millimeters) of *Tiramnia grunti*, n. sp. from GSC locality 56430.

GSC number	Length	Width	Thickness	Hingeline
115635	22.4	22.7	16.6	7.9
115636	20.1	19.9	14.9	8.6
115637	16.7	13.9	12.2	5.8

Genus *Jilinmartinia* Lee and Gu, 1980
? *Jilinmartinia* cf. *J. sokolovi* (Tschernyschew, 1902)
(Fig. 23.1–23.4)

- v.1902 *Spirifer sokolovi* Chernyshev, p. 166, pl. 8, fig. 3, pl. 39, fig. 4.
1939 *Spirifer (Brachythyris) sokolovi* Likharev, p. 107, pl. 27, fig. 3.
1980 *Martinia sokolovi* Kalashnikov, p. 100, pl. 36, fig. 2, 3; textfig. 10.

Discussion.—There is only one specimen of this species from GSC locality 56430. It is a large, completely smooth martiniid closely similar to the lectotype of *Spirifer sokolovi* Chernyshev (1902:pl. 8, fig. 3). The Canadian specimen has almost the same size, general shape, outline, regularly curved ventral valve, and nearly flat dorsal valve as seen in the Uralian specimen from the *Schwagerina* beds (Asselian) of Kazarmensky Kamen Hill near the town of Asha on the Sim River, Ural Mountains.

Comments.—Assignment of this species to the genus *Jilinmartinia* is uncertain because it is based only on external similarity with the type specimen of the type species. The internal morphology of the Chinese and Canadian specimens is unknown.

Kalashnikov (1980) reported *Martinia sokolovi* (Chernyshev) from the Lower Moscovian (Vereyan) and Upper Carboniferous beds of Novaya Zemlya and the Moscovian of north Timan. The specimen illustrated by Kalashnikov is more similar to specimens of *Jilinmartinia laevis* (Likharev, 1939) from the lower Gjelian of the Donets Basin.

Subfamily Eomartiniopsinae Carter, 1994
Genus *Heteraria* Cooper and Grant, 1976

Comments.—Cooper and Grant (1976) did not note the similarity of their new genus *Heteraria* to the Lower Carboniferous genera *Eomartiniopsis* Sokolskaya, 1941, or *Merospirifer* Reed, 1949. In the case of the former this was undoubtedly because of their misunderstanding of the dorsal interior of the type species of *Eomartiniopsis*, which was described by Sokolskaya as having short or incipient “septal” plates. In fact, there are no dorsal plates supporting the cardinalia in *Eomartiniopsis*. Thus, the dorsal interiors of *Eomartiniopsis*, *Merospirifer*, and *Heteraria* are similar. *Merospirifer* Reed, 1949, was recently redescribed by Brunton (1984) and appears to be similar to *Eomartiniopsis* in the dorsal interior. As far as we can determine, these genera can be internally differentiated only by the presence of unusually wide, transverse, flattened dental ridges in the ventral valve of *Heteraria* with narrow, more conventional ridges in *Eomartiniopsis* and *Merospirifer*.

There are only three Late Carboniferous eomartiniopsinine species known, *Eomartiniopsis planosinuata* Poletaev, 1975, from the early Bashkirian of the Donets Basin, *E.?* *susanae* Martinez-Chacon, 1978, from the middle to late Bash-

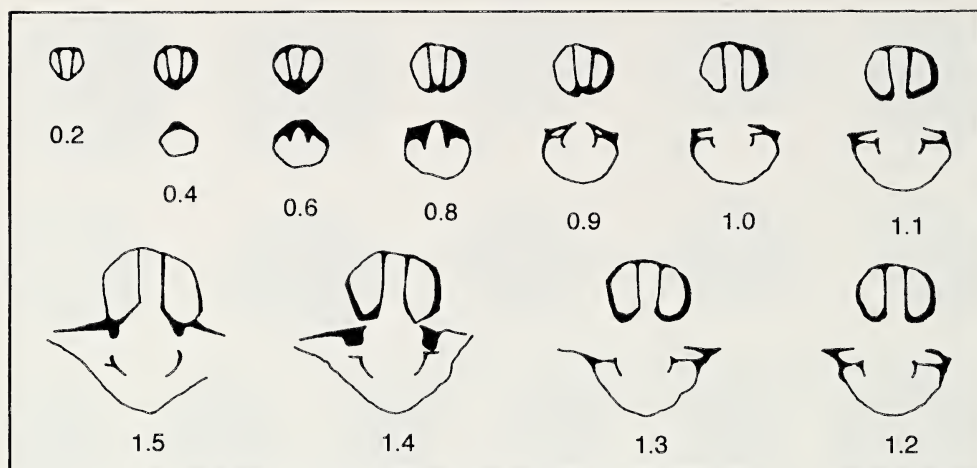


Fig. 22.—Transverse serial sections of ?*Heteraria canadiensis* n. sp., paratype, GSC 115643, from GSC locality 56430, $\times 3$. Numbers refer to distance in millimeters from ventral beak.

kirian of the Cantabrian Mountains, northern Spain, and the new species described below from the upper Bashkirian or lower Moscovian of Ellesmere Island. Their similarities and differences are discussed below.

?Heteraria canadiensis, new species
(Fig. 21.17–21.32, 22)

Holotype.—GSC 115640, Figures 21.18–21.22, from GSC locality 56430.

Paratypes.—GSC 115641, Figures 21.23–21.27, from GSC locality C-5202; GSC 115642, Figures 21.28–21.32, from GSC locality 56430; GSC 115639, Figure 21.17, micro-ornament, from GSC locality 56430A; Figure 22, GSC 115643.

Description.—Small to medium size for genus, smooth, thin shelled; transversely subovate or sub-pentagonal in outline; subequally biconvex, both valves considerably inflated; beaks small; hingeline narrow, half of maximum width; maximum width attained near midlength or slightly posterior to midlength; cardinal extremities rounded in all growth stages, but slightly angular in juveniles and delineated by obscure reflexing of outer surface of ventral valve; ornament consisting of irregularly spaced growth varices and some adult specimens have faint low costae or plicae on flanks; micro-ornament consisting of very small pits.

Ventral valve most convex in umbonal region; beak small and slightly incurved; sulcus originating as shallow groove posteriorly in umbonal region, becoming broader and deeper anteriorly, with angular borders and flattened floor; front margin strongly uniplicate with angular tongue; flanks gently convex or nearly flat; interarea moderately high, sharply defined, triangular; dental ridges (sensu Dunlop, 1962) very wide, flattened; deltidial or stegidial plates not observed; interior with short, slender, subparallel intrasinal dental adminicula.

Dorsal valve similar in convexity to ventral valve and almost as long; prominent umbo has small beak; fold poorly defined posteriorly, forming only low, rounded ridge, becoming well expressed only anteriorly; flanks slightly concave near the ears and gently convex otherwise; dorsal interarea low, acutely triangular, inconspicuous; interior with small ctenophoridium and narrow, vertical, medially concave crural bases which become broader and convergent anteriorly; other details not preserved in sectioned specimen.

Measurements.—See Table 18.

Diagnosis.—This species is characterized by its transversely subovate to sub-quadrate outline, almost equal thickness of the ventral and dorsal valves, small

Table 18.—*Measurements (in millimeters) of Heteraria canadiensis, n. sp.*

GSC number	Length	Width	Thickness	Hingeline
115640	>17.0	~21.0	14.5	~10.5
115641	13.6	16.2	9.4	~7.5
115642	11.1	12.3	8.1	6.2

ventral umbo with a short, narrow beak, deep flat-bottomed sulcus with anteriorly abrupt slopes, and very wide, flattened dental ridges.

Comments.—*Heteraria canadiensis* n. sp. resembles *Eomartiniopsis planosinuata* Poletaev, 1975, from the Lower Bashkirian of the Donets Basin. The Ukrainian species differs in its smaller size, very unequal convexity of ventral and dorsal valves, comparatively longer ventral umbo, higher interarea, and shallower sulcus than the Canadian species.

Eomartiniopsis susanae Martinez-Chacon, 1978, from the San Emiliano Formation (Bashkirian) of northern Spain, differs from *H. canadiensis* in having a roundly subquadrate outline with its greatest width at midlength or anterior to it, and a narrower sulcus with distinct grooves on the midline.

Distribution.—GSC locality 56430, four complete shells, two ventral valves, and one dorsal valve. GSC locality C-5202, two complete shells. GSC locality C-4085, one ventral valve. GSC locality 56430A, a well-preserved large ventral valve.

Indeterminate martinioid (Fig. 23.5–23.9)

Description.—Small, strongly and unequally biconvex with much thicker dorsal valve; outline subelliptical to rounded subpentagonal; lateral profile subelliptical, almost subovate; anterior profile thickly lenticular; sulcus well developed but fold scarcely discernible; anterior commissure strongly uniplicate; surfaces smooth except for very faint, widely spaced radial lirae and fine growth lines, the former possibly reflecting internal vascular markings.

Ventral valve shorter and much thinner than dorsal valve; umbonal region moderately convex, defined by strongly concave lateral flexures, forming compressed posterolateral margins; beak very small, incurved; delthyrium open, small, triangular; interarea small, narrow, procline, triangular, weakly delineated by scarcely perceptible beak ridges; lateral slopes gently concave, sloping evenly to lateral margins; sulcus originating in umbonal region, becoming smoothly rounded and moderately deep and wide anteriorly; interior unknown.

Dorsal valve very thick, strongly inflated, with moderately swollen umbonal region delineated by concave flexures that are less concave than those of opposite valve; dorsum strongly convex, lateral slopes more gently convex, sloping evenly to lateral margins; fold confined to very slight dorsal deflection of shell surface near anterior margin; interarea very short and narrow, about orthocline; interior unknown.

Comments.—We little doubt that this shell represents an adult individual because of the well-developed sulcus and rotund shape. The translucent shell material provides no suggestion of internal structures in either valve. Growth form, lack of ornamentation, and probable lack of internal plates indicate that this small shell is undoubtedly a martinioid of some kind. However, the short ventral valve with procline ventral interarea, greatly swollen dorsal valve, and unusual micro-ornament preclude assignment to a known species, genus, or even family.

Distribution.—GSC locality 56430 (one specimen).

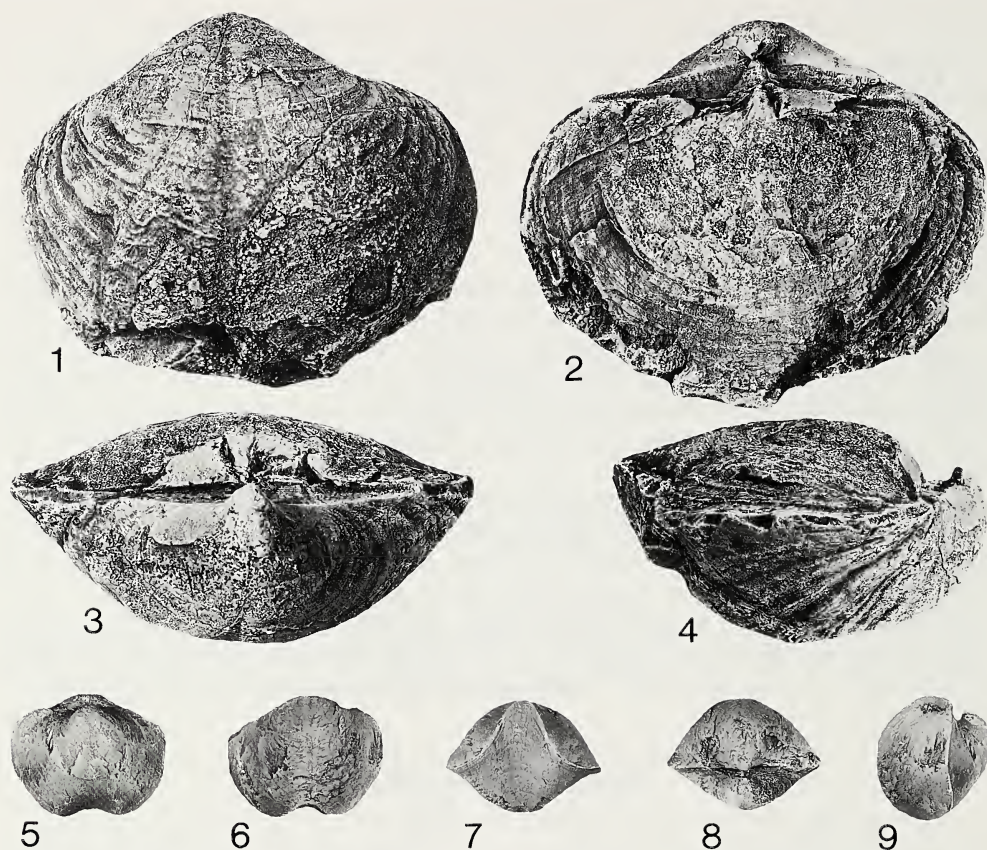


Fig. 23.—Martinioids. 23.1–23.4, *?Jilinmartinia* cf. *J. sokolovi* (Chernyshev, 1902), ventral, dorsal, posterior, and lateral views, GSC 115644, $\times 1$. 23.5–23.9, indeterminate martinioid, ventral, dorsal, anterior, posterior, and lateral views, GSC 115645, $\times 2$.

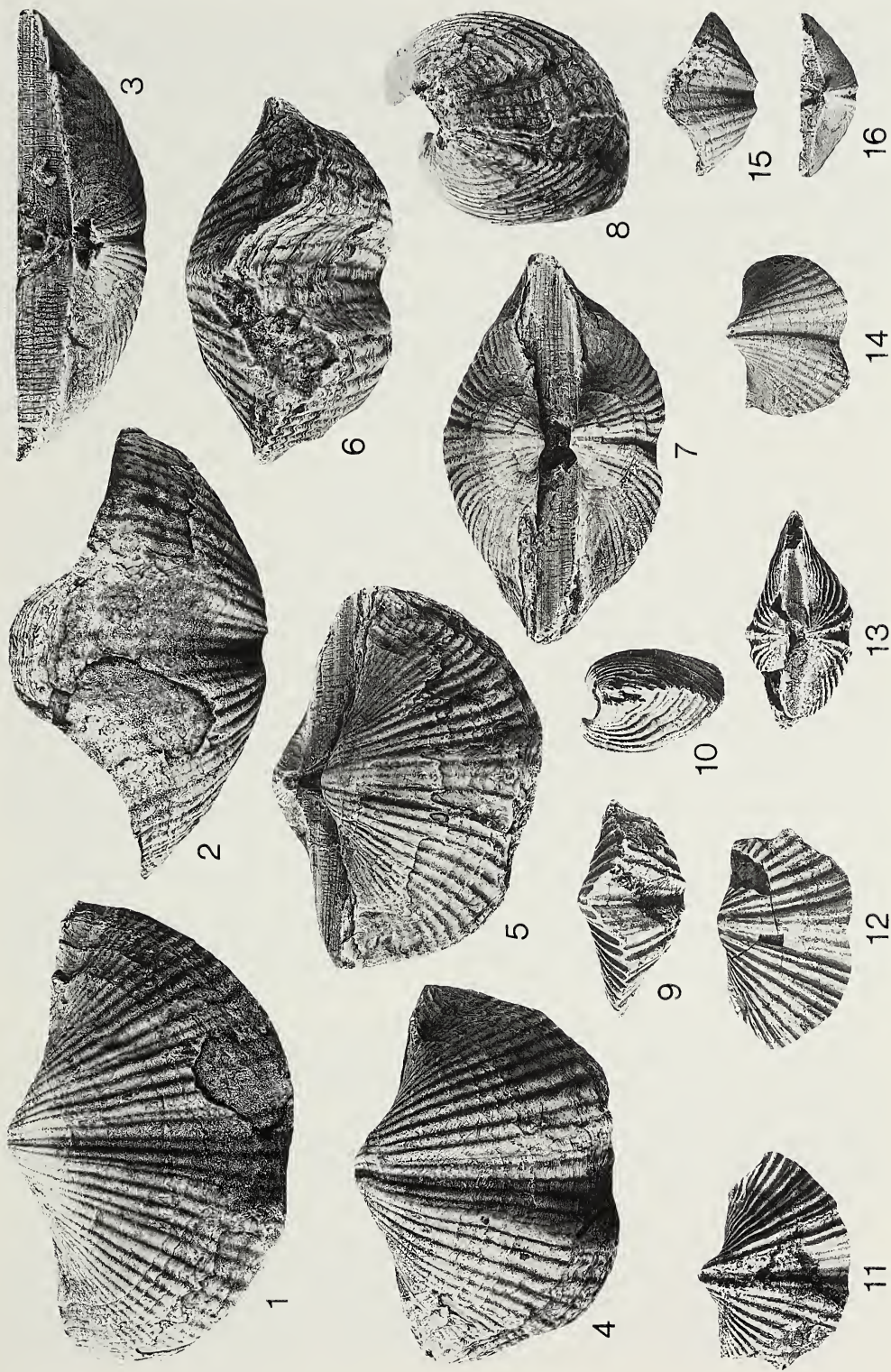
Superfamily Spiriferoidea King, 1846
 Family Spiriferidae King, 1846
 Subfamily Sergospiriferinae Carter, 1994
 Genus *Anthracospirifer* Lane, 1963
Anthracospirifer cf. *A. occiduus* Sadlick, 1960
 (Fig. 24.9–24.13)

1960 *Spirifer occiduus* Sadlick, p. 1210.

Description.—This description is based on two specimens from GSC locality 56430. An almost complete shell with incomplete cardinal extremities measures approximately 37 to 38 mm in width, 22.7 mm in length, and 15.8 mm in thickness. The remaining specimen is a small ventral valve.

→

Fig. 24.—Spiriferoids. 24.1–24.8, *Elinoria ellesmerensis* n. sp.; 24.1–24.3, ventral, anterior, and posterior views of a large ventral valve, GSC 115646; 24.4–24.8, ventral, dorsal, anterior, posterior, and lateral views of the holotype, GSC 115647, $\times 1$. 24.9–24.13, *Anthracospirifer* cf. *A. occiduus* Sadlick, 1960, anterior, lateral, ventral, dorsal, and posterior views, GSC 115648, $\times 1$; 24.14–24.16, *?Brachythyrina* sp., ventral, anterior, and posterior views of a ventral valve, GSC 115649, $\times 1$.



Ventral valve with short, narrow ventral umbo, moderately high, triangular interarea, deep V-shaped sulcus with obvious median rib and three ribs on each side of sulcus, up to 14 or 15 ribs on each flank, four or five of them bifurcated.

Dorsal valve with short, strongly incurved umbo, narrow acute interarea, prominent fold with groove on midline, and four or five bifurcated ribs on each flank.

Remarks.—This shell is similar in general shape and ribbing to the lectotype of *Anthracospirifer occiduus* (Sadlick), as illustrated by Girty (1927) and Gordon (1975). The shell from Ellesmere Island differs from the lectotype in having a higher ventral interarea and concave lateral slopes on the ventral valve and gently convex flanks on the dorsal valve.

Family Choristitidae Waterhouse, 1968
Subfamily Angiospiriferinae Legrand-Blain, 1985
Genus *Elinoria* Cooper and Muir-Wood, 1951
Elinoria ellesmerensis, **new species**
(Fig. 24.1–24.8)

Holotype.—GSC 115647, Figures 24.4–24.8, from GSC locality 56430.

Paratypes.—GSC 115646, Figures 24.1–24.3, a large ventral valve from GSC locality 60194.

Description.—Medium to large, subequally biconvex; outline transversely subovate to subsemicircular in early growth stages, becoming subtrapezoidal in adults; cardinal extremities alate to submucronate; sulcus moderately wide and deep, well defined; fold low, rounded, sharply delineated; anterior commissure uniplicate; flanks with few, simple, low, rounded costae, separated by narrow interspaces, and strong, irregularly spaced growth varices; width of costae varies from 0.6 to 0.8 mm near umbo, up to 3.0 mm or more near anterior margin; micro-ornament consisting of fine concentric growth lines and capillae; shell substance of moderate thickness for genus, reaching 3.0 mm thick in ventral umbo.

Ventral valve moderately to strongly inflated with greatest convexity near or posterior to midvalve; surface of valve regularly convex except for sulcus and slight flexure near ears; umbo comparatively short and umbonal angle usually about 110 degrees; interarea flat or slightly concave and of moderate height, vertically grooved, abruptly truncated laterally, apsacline to nearly catacline; delthyrium forming equilateral triangle, or slightly higher than wide, open; sulcus subtending angle of about 30 degrees; sulcus with strong median costa, one pair of strong lateral sulcal costae which also originate at beak, and two or three pairs of weak, flat costae bifurcating from sulcus-bounding costae; sulcus spreading anteriorly in some large specimens to incorporate one or two pairs of costae from lateral slopes; lateral slopes with about 15 simple, rounded costae at anterior margin of each flank in adult specimens.

Ventral interior lacking dental plates, bearing deep, narrow, depressed muscelscar with short partial myophragm.

Dorsal valve less inflated than opposite valve, forming semicircular anterior profile; dorsal umbo blunt, beak small, incurved; interarea orthocline, low, with acute extremities; fold low and clearly delineated, usually bearing four costae, flatter than those of lateral slopes; lateral costae simple, excluding those nearest fold; dorsal interior unknown.

Measurements.—See Table 19.

Diagnosis.—The large size, transversely subtrapezoidal outline, clearly defined sulcus, coarse simple costae, and absence of dental plates distinguish this species from other Hare Fiord spiriferids.

Comparisons.—*Elinoria ellesmerensis* n. sp. is most similar to *E. rectangula* (Kutorga) sensu Chernyshev (1902), from the Lower Permian (Asselian) of the

Table 19.—*Measurements (in millimeters) of Elinoria ellesmerensis, n. sp.*

GSC number	Length	Width	Thickness	Hingeline
115646	45.7	69.2	20.5	64.1
115647	41.3	57.0	34.1	55.3

western slope of the middle Urals. The Canadian species differs from the Russian one in its thicker, more stout shell, narrower width, a higher interarea in adults, mucronate cardinal extremities in juveniles, and simple or very rarely bifurcating lateral costae. Two other similar Russian species are *Elinoria kremenskensis* (Semikhatova, 1953) from the Upper Moscovian and Kasimovian of the Don-Medveditsa district, and *E. subgrandis* Poletaev, 1986, from the lower Gjelian of the Donets Basin and Samarskaya Luka on the middle Volga River. *Elinoria kremenskensis* is much smaller, almost half the size, lacks mucronate cardinal extremities, has a poorly delineated sulcus, and often has bifurcated costae on the lateral slopes. *Elinoria subgrandis* differs in its less inflated profile, semicircular to subquadrate outline, and has bifurcating costae on the lateral slopes.

Distribution.—GSC locality 56430 (four specimens, two complete, including the holotype); GSC locality C-4083 (three more or less complete small ventral valves); GSC locality 60194 (one large ventral valve paratype and one small complete shell). A similar or identical species occurs in the Ladrões Limestone of southeastern Alaska.

Genus *Brachythyryna* Frederiks, 1929

?*Brachythyryna* sp.

(Fig. 24.14–24.16)

Description.—This description is based on a single ventral valve from GSC locality C-4087.

Medium size for genus (length 19.8 mm, width 24.4 mm, thickness 10.7 mm), moderately inflated, most convex in umbonal region; outline transversely subtrapezoidal; anterior commissure uniplicate; greatest width at hingeline; lateral extremities subangular, slightly mucronate and compressed in adult and transversely subovate in juveniles; beak small, narrow, incurved; beak ridges inconspicuous on umbo, angular and well defined near ears; interarea acutely triangular, weakly to moderately concave, of moderate height, catacline, vertically grooved; hingeline denticulate; delthyrium slightly higher than wide, apparently open; sulcus strong, well defined, moderately wide and deep, rounded; median sulcal costa very weak, originating in umbonal region; two pairs of lateral sulcal costae originating by bifurcating from sulcus-bounding costae, remaining simple for entire length; macro-ornament consisting of eight to ten simple, low, flattened, rounded costae on each flank and rare irregular growth varices; micro-ornament consisting of fine, regularly spaced growth lines; capillae not observed; umbonal region thickened with callus; inner structures not observed.

Comments.—This specimen was assigned to *Brachythyryna* because it has the external characters of that genus and because it is externally similar to the Middle–Upper Bashkirian species *Spirifer (Brachythyryna) probus* Rotai, 1951, from the Donets Basin and *Brachythyryna pinica* Martinez-Chacon, 1978, from the Cantabrian Mountains, northern Spain.

Subfamily Choristitinae Waterhouse, 1968

Genus *Parachoristites* Barchatova, 1970

Parachoristites tellevakensis, new species

(Fig. 25.1–25.15)

Holotype.—A nearly complete shell with incomplete cardinal extremities, GSC 115650, Figures 25.1–25.5, collected by Bonham-Carter at GSC locality 60194.

Paratypes.—Two almost complete shells, GSC 115651 and 115652, Figures 25.6–25.15, from the same locality as the holotype.

Description.—Medium to large; outline subtriangular, transversely subrhomboidal, or subsemicircular; hingeline equal to or only slightly shorter than greatest width in shells with moderately large and incurved ventral beak; greatest thickness located near midlength; ventral valve slightly thicker than dorsal; ventral interarea high or moderately high for genus, with distinct vertical grooves and truncated lateral extremities; sulcus weakly developed, shallow, narrow, poorly defined; anterior com-

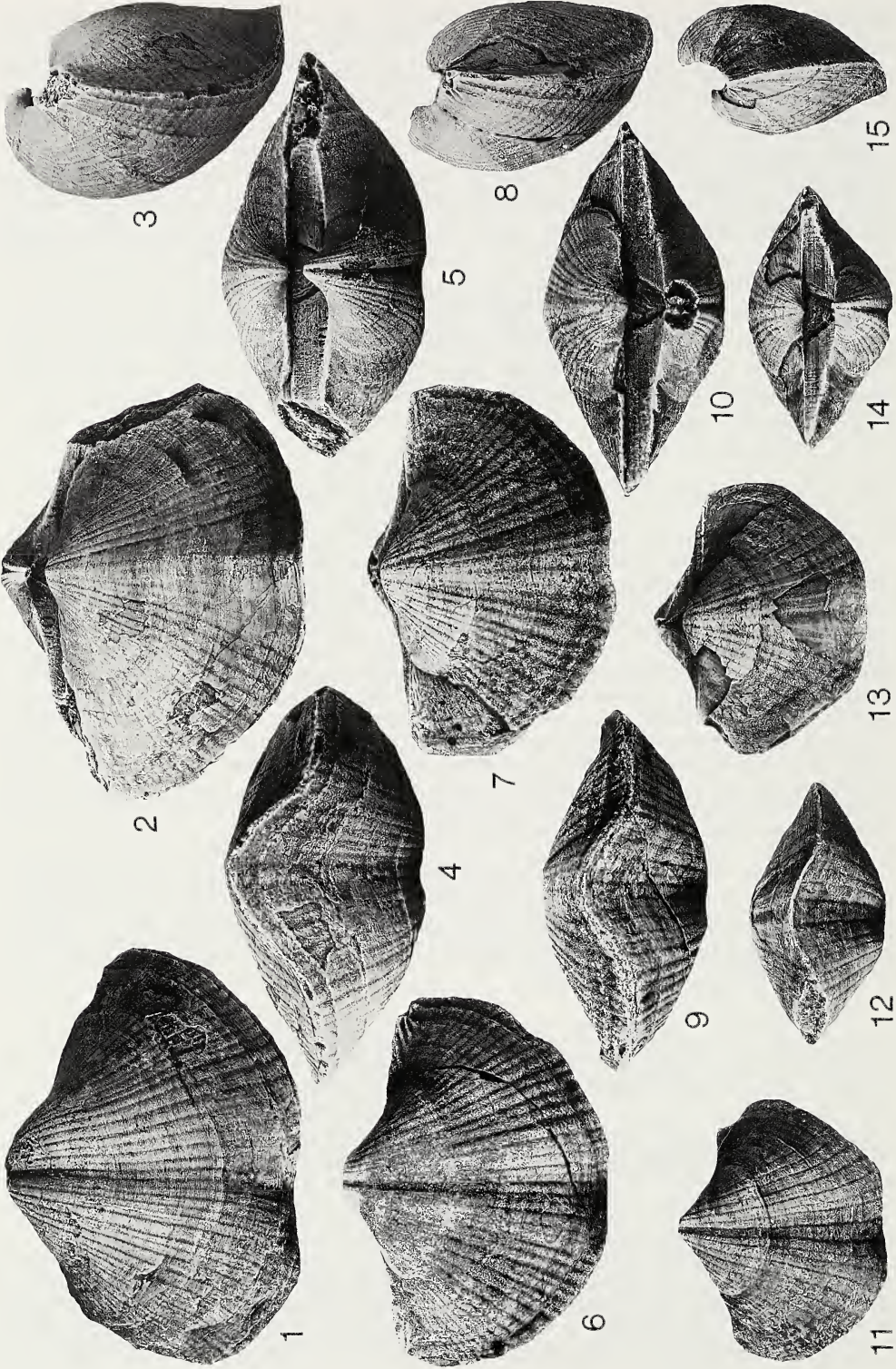


Table 20.—Measurements (in millimeters) of the types of *Parachoristites tellevakensis*, n. sp. from GSC locality 60194.

GSC number	Length	Width	Thickness	Hingeline
115650	47.4	~70.0	31.8	—
115651	>40.3	54.5	27.1	51.6
115652	31.8	39.5	21.3	~34.8

missure usually clearly uniplicate; fold very low and rounded posteriorly but clearly defined and elevated anteriorly; macro-ornament consisting of numerous flattened, rounded costae, mostly irregularly bifurcated or trifurcated, with 11 to 13 costae in anterior part of sulcus, including very weak median rib, and up to 20 costae on each lateral slope; costae separated by narrow interspaces and sometimes crossed by strong, irregularly spaced growth varices; micro-ornament consisting of fine capillae and fine regular growth lines.

Ventral valve most convex in umbonal region; beak of small to moderate size, incurved, overhanging hingeline; umbonal region moderately broad with umbonal angle of about 95 to 100 degrees; flanks gently convex; lateral extremities slightly compressed on ears, forming sharp beak ridges; sulcus originating at beak, flat and shallow, becoming wider and deeper anteriorly, producing moderate tongue; interarea apsacline, clearly triangular, concave in juveniles, becoming flat with nearly parallel sides at maturity, and abruptly truncated extremities; delthyrium open, triangular, higher than wide, deltidial plates not observed; interior with thick, weakly diverging, moderately long dental adminicula which reach almost one-quarter length of valve; delthyrial plates conjoin in beak, becoming free anteriorly and including between them muscle impressions; posterior inner surface of the valve with traces of bifurcating vascular impressions.

Dorsal valve usually semicircular in outline, moderately convex with short incurved umbo and low subparallel interarea; fold low, medially flattened, rounded, clearly defined, with shallow midline groove and six to ten obscure costae at anterior margin; lateral slopes with 18 to 20 ribs on each side, most of which bifurcate; interior with ctenophoridium composed of numerous plates.

Measurements.—See Table 20.

Diagnosis.—This species is distinguished by its large size, comparatively high ventral interarea with sharp beak ridges in young stages; weak shallow sulcus with obscure borders; low, rounded, clearly defined fold; low, flat, irregularly bifurcating costae, and moderately long, thick, subparallel dental adminicula.

Comments.—*Parachoristites tellevakensis* n. sp. bears similarity to the type species, *P. volongaensis* Barkhatova, 1970, from the Bashkirian of the Volonga River and north Timan (Russia). The Canadian species differs in usually being smaller with a longer more subrhomboidal outline, a higher subtriangular ventral interarea, more elevated fold anteriorly, and flatter costae.

Parachoristites tellevakensis n. sp. has some similarity to two other species of large spiriferids from the Televak Limestone Member. The species we refer to here as *?Trautscholdia* sp., from GSC locality C-56430, differs in its transversely subovate outline, absence of mucronate cardinal extremities, low subparallel ventral interarea, very weak sulcus with medial groove, very weak tongue, almost flat dorsal valve, and a fold defined only by deep interspaces.

Elinoria ellesmerensis n. sp. differs in having a high subparallel ventral interarea; a strong, clearly restricted sulcus; simple coarse costae; and no dental adminicula.

←

Fig. 25.—Spiriferoids. 25.1–25.15, *Parachoristites tellevakensis* n. sp., ventral, dorsal, lateral, anterior, and posterior views of three specimens, including the holotype (25.1–25.5), GSC 115650–115652, respectively, $\times 1$.

Distribution.—This species is moderately common at GSC locality 60194 (27 complete specimens) and GSC locality 56430 (more than 12 complete specimens, plus disarticulated valves).

Genus *Trautscholdia* Ustritsky, 1967

?*Trautscholdia* sp.

(Fig. 26.2–26.6)

Description.—This description is based on a single large specimen (length 48.4 mm, width 66.2 mm, thickness 29.5 mm), from GSC locality 56430.

Large, ventribiconvex, transversely subovate in outline with moderately thick ventral and weakly convex dorsal valves; cardinal extremities rounded on all growth stages; maximum width attained near midlength; ventral interarea low, acutely triangular, apsacline, concave; hingeline slightly shorter than greatest width, denticulate; sulcus very weak, narrow, poorly defined, medially grooved; lateral slopes with up to 30 wide, low, flattened, rounded costae at anterior margin, mostly simple or irregularly bifurcating or, rarely, trifurcating; growth varices irregularly spaced; micro-ornament consisting of strong capillae, about eight to ten per mm, and very fine, regularly spaced growth lines forming cancellate pattern; both valves much thickened posteriorly; ventral interior with nearly parallel dental adminicula.

Comments.—This specimen is similar to *Choristites jigulensis* (Stuckenberg, 1905) sensu Ivanov and Ivanova, 1937 (pl. 11, fig. 1 and pl. 12, fig. 1) from the Upper Moscovian (Podolsky Horizon) of Shchurovo village, Moscow Basin. However, the Upper Moscovian specimens and the specimen from Ellesmere Island differ from the lectotype in the outline of their shells. The lectotype of *Spirifer jigulensis* Stuckenberg, 1905, is from the Lower Gjelian of the Samarskaya Luka (Volga River near the city of Samara). This lectotype has a subquadrate, not a transversely subovate, outline; a shorter hingeline; and a longer ventral umbo than either the Russian Upper Moscovian specimens or the specimen from Ellesmere Island.

Trautscholdia jigulensis (Stuckenberg, 1905), in the junior author's opinion, has many synonyms, including other species described by Stuckenberg from the type locality at Samarskaya Luka. We do not include Upper Moscovian specimens in the synonymy of *T. jigulensis* (Stuckenberg). It is possible that the specimens of Moscovian age represent a cognate but different, perhaps undescribed, species.

Subfamily Tangshanellinae Carter, 1994

Genus *Tangshanella* Chao, 1929

?*Tangshanella* sp.

(Fig. 26.7–26.9)

Description.—This description is based on a single incomplete specimen from GSC locality 56430.

Medium size (length 38.3 mm, width 44.4 mm, thickness 23.5 mm), moderately inflated, ventribiconvex; outline transversely subovate in all growth stages; ventral umbo narrow, moderately inflated, and extended; cardinal extremities and lateral margins well rounded, hingeline very narrow (15.2 mm), about one-third maximum width; sulcus shallow, poorly defined, with weak groove in midline; fold low, poorly delineated, expressed only anteriorly, producing uniplicate anterior commissure; costae wide, low, roundly flattened, mostly bifurcating but almost disappearing at posterolateral margins; growth varices coarse, rare, irregular; micro-ornament not observed.

Ventral valve twice as thick as dorsal valve, moderately and regularly convex with maximum width at midlength; interarea apsacline, moderately high, triangular; delthyrium open, wider than sides of interarea; hingeline very narrow, denticulation not observed; sulcus with three pairs of primary costae, weak median costa, which begins much later than primary costae; all primary costae usually bifurcate anteriorly; dental adminicula either very short or absent (beak lost).

Dorsal valve subovate, very gently convex, with small, prominent umbo, low, almost linear, dorsal interarea, and wide notothyrium; interior not observed.

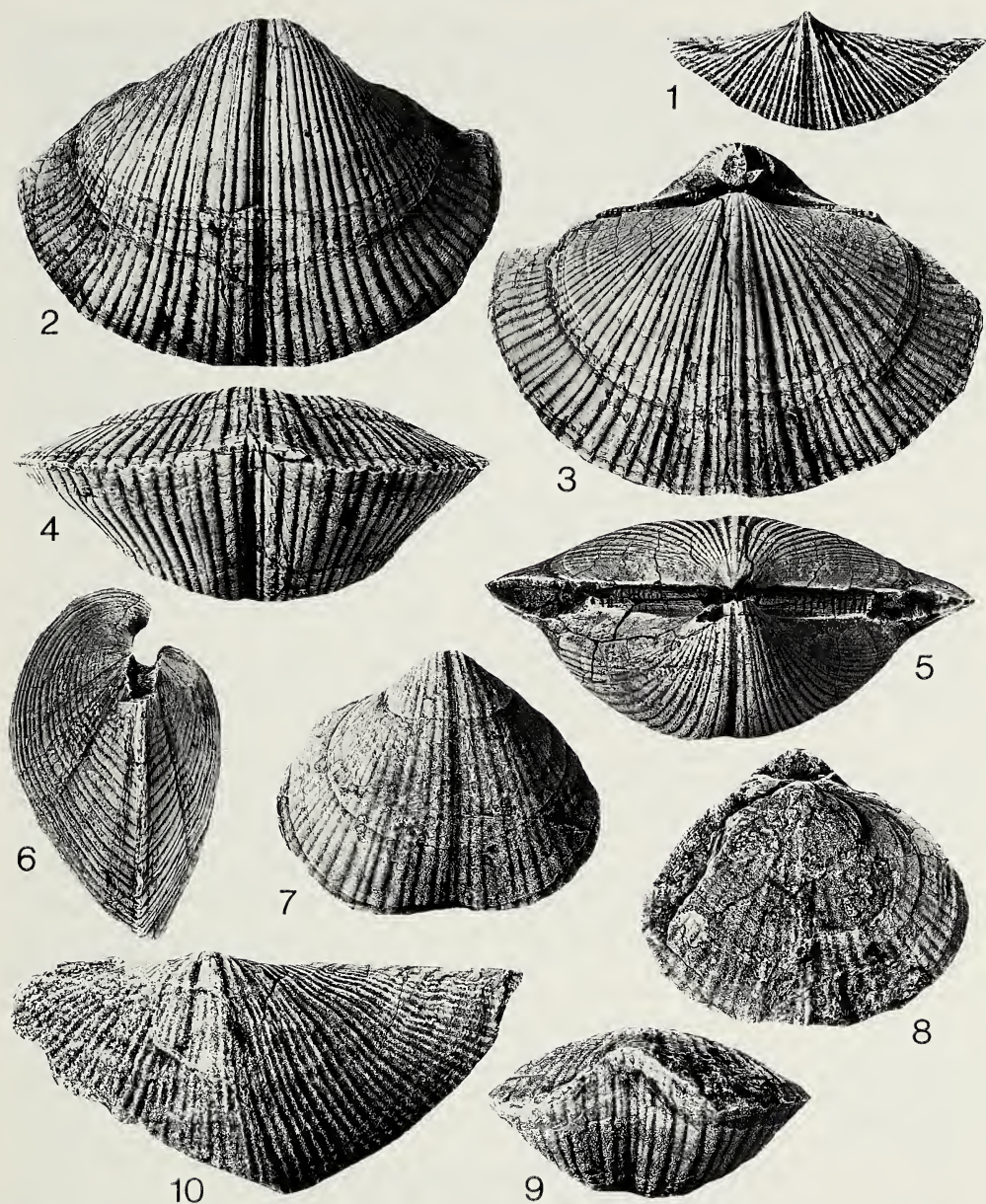


Fig. 26.—Spiriferoids. 26.1, 26.10, *Gypospirifer* sp.; 26.1, a small ventral valve, GSC 115653; 26.10, a large dorsal valve, GSC 115656. 26.2–26.6, *?Trautscholdia* sp., ventral, dorsal, anterior, posterior, and lateral views, GSC 115654. 26.7–26.9, *?Tangshanella* sp., ventral, dorsal, and anterior views, GSC 115655. All $\times 1$.

Diagnosis.—The transversely subovate outline, extremely narrow hingeline, wide, roundly flattened commonly bifurcating costae, shallow, poorly delimited sulcus and weak fold, and possible lack of dental adminicula serve to differentiate this species from all other spiriferids in the Televak Limestone Member.

Comments.—This Canadian specimen differs from the other representatives of the genus *Tangshanella* Chao, 1929. The type species, *T. kaipingensis* Chao, from the Tangshan Limestone of the Penchi Series (Upper Carboniferous) of north China, differs in having a thicker shell with a much stronger sulcus and fold, a wider hingeline, and a higher ventral interarea. *Tangshanella taimyrica* (Einor, 1939), from the Makarovsky Horizon (Bashkirian) of Taimyr, and *T. byrangi* Cherniak, 1963 (in Ustritskii and Cherniak, 1963), from the Kholodninskaya Suite (Bashkirian) of Taimyr, have wider ventral interareas, and clearly fasciculate, strong, thin costae. They may not belong in this genus.

This ?*Tangshanella* sp. from the lower Hare Fiord Formation is similar in outline, growth form, ribbing, and foldsulcus to *Neomunella* Ozaki, 1931, from the Pen-hsi-hsien (Upper Carboniferous) of Manchuria (north China). However, the latter has short, distinct, divergent dental plates. We assign our specimen to the genus *Tangshanella* with a query (?) because we cannot determine whether or not there were short dental adminicula in this incomplete specimen.

Family Trigonotretidae Schuchert, 1893
Subfamily Neospiriferinae Waterhouse, 1968
Genus *Gypospirifer* Cooper and Grant, 1976
Gypospirifer sp.
(Fig. 26.1, 26.10)

Description.—This description is based on two specimens. A small ventral valve, perhaps a juvenile, and a large dorsal valve were collected at GSC locality 56430.

Ventral valve moderately convex, strongly transverse with maximum width at hingeline; cardinal extremities slightly mucronate, slender (length 15.2 mm, width 43.3+ mm, complete width probably close to 50.0 mm, thickness ~8.0 mm); commissure uniplicate; beak short, incurved, not swollen; sulcus shallow, well delineated by bounding costae and producing angle near 25 degrees; interarea triangular, comparatively high (approximately one-third valve length), slightly concave, strongly vertically grooved; delthyrium as high as wide, open or partly closed by stegidial plates; costae fine, bifurcated or trifurcated only in umbonal region, anteriorly simple, numbering ten per cm near anterior commissure; sulcus with median costa originating at beak; two pairs of costae, split from bounding costae inside sulcus, one pair split outside; growth lamellae distinct, regularly spaced, slightly raised to give regulate appearance.

Dorsal valve of average size (length 33.4 mm, width >67.2 mm, probably about 85 to 90 mm when complete); outline transversely semicircular with maximum width at hingeline; dorsum moderately convex; maximum thickness in umbonal region; flanks weakly convex with slightly compressed ears; cardinal extremities acute and mucronate in all growth stages; fold gently rounded, not raised much above flanks; costae medium size (eight per cm near anterior commissure), rounded, separated by rounded interspaces, 26 to 28 on flanks, mostly trifurcating from five to six primary ribs on umbo; ten costae on fold, bifurcating from median rib; growth varices numerous, regular; interior and micro-ornament not observed.

Superfamily Paeckelmanelloidea Ivanova, 1972
Family Strophopleuridae Carter, 1974
Subfamily Strophopleurinae Carter, 1974
Genus *Cantabriella* Martinez-Chacon and Rio Garcia, 1987

This genus was assigned originally to the Licharewiidae by Martinez-Chacon and Rio Garcia (1987). However, the type species, *Orulganina schulzi* Martinez-Chacon, 1978, is impunctate according to Martinez-Chacon (1978). The pits described later by Martinez-Chacon and Rio Garcia (1987:pl. 1) appear to be an artifact of chemical corrosion. The type species of *Cantabriella* clearly has affinities with the paeckelmanellids, having such characters as disproportionately strong sulcus-bounding ribs, high ventral interarea, noncostate foldsulcus; strongly

denticulate hingeline, close-set, intrasinal dental adminicula, and capillate micro-ornament.

The authors of this genus included three species, all the from the Upper Carboniferous of Spain: *Cantabriella schulzi* (Martinez-Chacon, 1978) from Upper Bashkirian of Leon and Asturias; *C. palentina* (Martinez-Chacon, 1978) from Upper Moscovian of Palencia, and *C. lavianica* Martinez-Chacon, 1987, from Lower Moscovian of Asturias. In our opinion *Spirifer* (*Syringothyris*?) *bistritzae* Schellwien, 1900, from the Trogkofel shales (?Lower Permian) of the Carnic Alps of northern Slavonia also can to be assigned to this genus.

Cantabriella sp. A
(Fig. 27.6–27.10)

Description.—This description is based on a single, nearly complete, possibly slightly deformed shell collected at GSC locality 56430.

Medium size (length 13.6 mm, width >20.0 mm, thickness 11.1 mm), subequally biconvex, transversely subpentagonal in outline; lateral extremities acute and angular in all growth stages, becoming almost rectangular in adults; maximum width attained at hingeline; sulcus well developed and defined; anterior commissure uniplicate; ornament consisting of seven to eight simple, rounded, flattened costae on flanks; sulcus and fold smooth with weak, shallow furrow on midline; micro-ornament consisting of weak, irregularly spaced growth varices, very faint regularly and closely spaced growth lines, crossed by comparatively coarse capillae.

Ventral valve subpyramidal with maximum thickness in umbo; beak small, acute, incurved; ventral interarea high, procline, concave only near beak, weakly defined by rounded beak ridges, grooved by strong vertical furrows; delthyrium moderately broad but higher than wide; deltidial plates not observed; sulcus originating at beak as narrow groove bordered by pair of wide costae, becoming wider and deeper anteriorly, producing flattened, long tongue in anterior third of valve; interior with dental adminicula.

Dorsal valve transversely semicircular to subelliptical in outline, most convex in umbonal region, nearly as thick as ventral valve, reaching maximum thickness near midlength; umbo slightly swollen; beak small, inconspicuous; fold defined only by bounding interspaces posteriorly, becoming slightly raised anteriorly from midlength; internal details not observed.

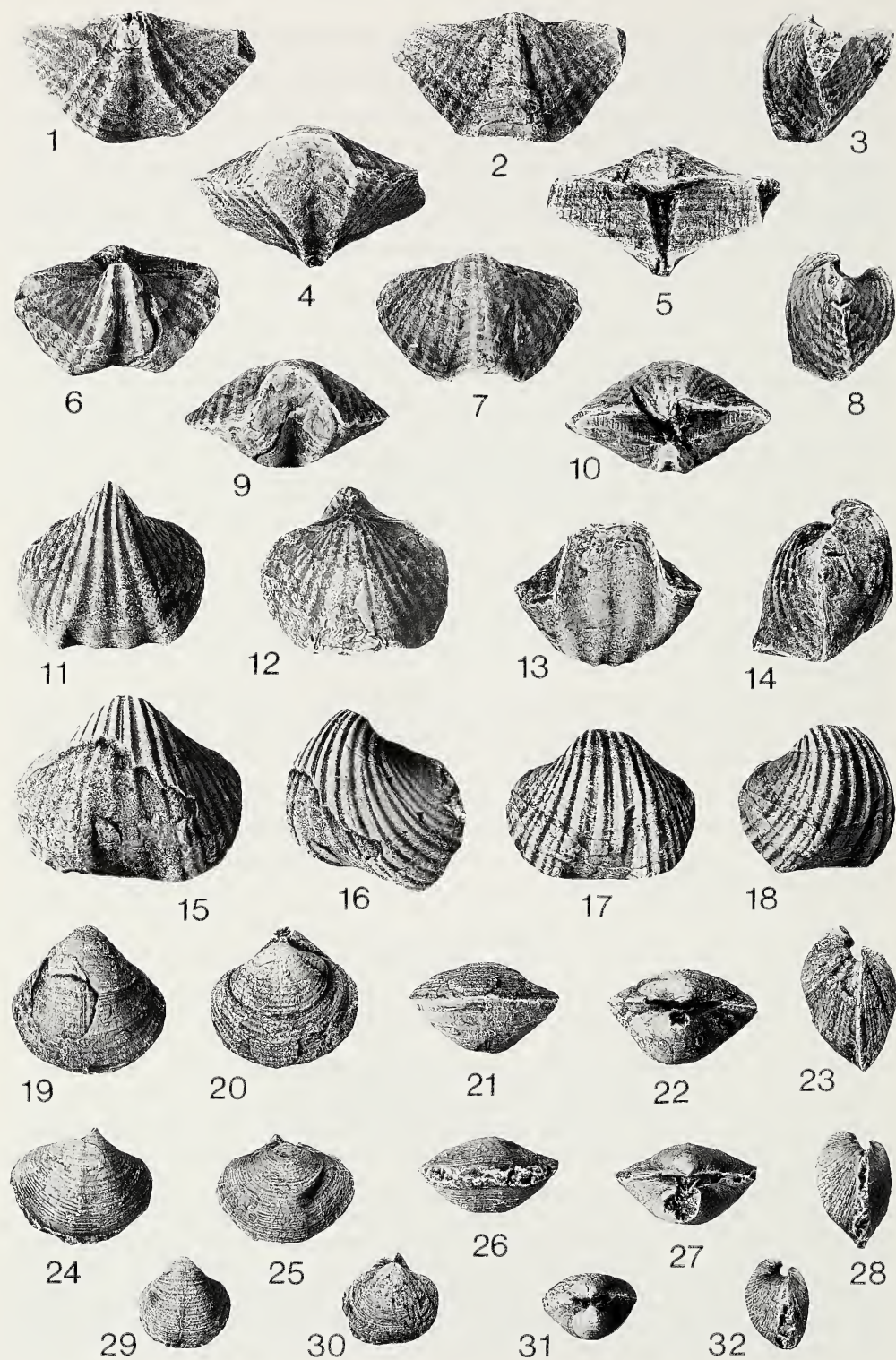
Diagnosis.—The subpentagonal outline, almost equal thickness of the subpyramidal ventral and swollen dorsal valves, procline ventral interarea, and simple costae rapidly decreasing to size toward the ears are the most characteristic features of this specimen.

Cantabriella sp. B
(Fig. 27.1–27.5)

Description.—This description is based on a single, almost complete shell with broken cardinal extremities, spalled surface, but well-preserved growth form, from GSC locality C-4085.

Medium size (length 15.7 mm, width >23.0 mm, thickness 10.6 mm); very unequally ventribiconvex; transversely subtriangular in outline; lateral extremities angular in all growth stages; maximum width attained at hingeline; sulcus and fold well developed and defined; anterior commissure uniplicate; ornament consisting of from nine to 11 rounded, flattened costae on flanks, broad near foldsulcus, becoming much finer laterally; bounding costae bifurcate on one side only; fold and sulcus smooth; sulcus with subangular floor; micro-ornament not preserved but consisting at least of more or less regularly spaced growth varices.

Ventral valve subpyramidal, much thicker than dorsal valve, with maximum thickness in umbonal region; flanks concave, sloping evenly to anterolateral margins; ears compressed; umbonal region narrowly elongated; beak small, acute, slightly incurved; ventral interarea high, catacline or nearly procline, generally flat, weakly concave near beak, defined by sharp beak ridges; surface of interarea with strong vertical grooves; delthyrium narrow, almost three times higher than wide; subdelthyrial plate long, set well below surface of interarea between close-set intrasinal dental adminicula; stegidial plates not observed; sulcus comparatively shallow, originating as narrow groove, becoming wider and deeper anteriorly, defined by strong bounding costae.



Dorsal valve transversely trapezoidal in outline, with maximum thickness at midlength, much thinner than opposite valve; umbo slightly produced above beak ridges; middle part of valve slightly convex or swollen from beak to front commissure; flanks concave, ears compressed; fold originating at small beak, well defined by bounding interspaces, slightly flattened medially near anterior margin; internal details not observed.

Diagnosis.—This specimen probably also represents a new species of this genus, differing from other species of *Cantabriella* in having a transversely triangular outline, concave flanks, elongated and compressed ears, and nine to 11 ribs on each flank.

Superfamily Brachythyridoidea Frederiks, 1924

Family Brachythyrididae Frederiks, 1924

Genus *Meristorygma* Carter, 1974

Meristorygma arctica Carter, 1974

(Fig. 27.11–27.14)

v*1974 *Meristorygma arctica* Carter, p. 690, pl. 3, fig. 21–30; text-fig. 4.

Original Diagnosis.—“This species is characterized by its transversely ovate outline, compressed lateral extremities, two or four sulcal costae, and dorsally deflected fold at the anterior margin.”

Comments.—This species was originally described on the basis of eight specimens from GSC locality 56430. Our present collection contains nearly 100 specimens, many complete, from the same locality.

Some natural molds of the ventral valves show that the type species of *Meristorygma* has a ramose, radially arranged vascular system surrounding the muscle field with a pair of strong vascula media, which approximately correspond to the strongest pair of costae in the sulcus. The distinctive vascular system in this genus constitutes an important difference between it and *Brachythyris*, because the latter has a weak, simple, radial, *Martinia*-like vascular system.

Distribution.—In addition to the large collection from GSC locality 56430 there is one incomplete specimen from GSC locality C-4087 and four specimens from GSC locality 56430A. A similar species occurs in the Ladrone Limestone of southeastern Alaska.

Meristorygma, new species A

(Fig. 27.15–27.18)

Two disarticulated ventral valves of *Meristorygma* sp. from GSC locality 56430A preserve the general shape and most other characters of *Meristorygma arctica* Carter, 1974, but differ distinctly from that species in having four to five clearly expressed bifurcating costae on both flanks and a very thin, weak median

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Fig. 27.—Paeckelmannelloids, brachythyridoids, and reticularioids. 27.1–27.5, *Cantabriella* sp. B, ventral, dorsal, lateral, anterior, and posterior views, GSC 115657, $\times 1.5$. 27.6–27.10, *Cantabriella* sp. A, ventral, dorsal, lateral, anterior, and posterior views, GSC 115658, $\times 1.5$. 27.11–27.14, *Meristorygma arctica* Carter, 1974, ventral, dorsal, anterior, and lateral views, GSC 115659, $\times 1$. 27.15–27.18, *Meristorygma* n. sp. A, ventral and oblique views of two ventral valves, GSC 115660 and 115661, $\times 1$. 27.19–27.32, *Phricodothyris asiatica* (Chao, 1929), ventral, dorsal, anterior, posterior, and lateral views of three specimens, GSC 115662–115664, respectively, $\times 1$.

rib in the sulcus. Obviously these specimens represent a different, perhaps new, species but the lack of specimens prevents us from describing it.

Suborder Delthyridina Ivanova, 1972
 Superfamily Reticularioidea Waagen, 1883
 Family Elythidae Frederiks, 1924
 Subfamily Phricodothyridinae Caster, 1939
 Genus *Phricodothyris* George, 1932
Phricodothyris asiatica (Chao, 1929)
 (Fig. 27.19–27.32)

1902 *Reticularia lineata* Martin: Chernyshev, p. 193, pl. 20, fig. 9–13.

1929 *Squamularia asiatica* Chao, p. 91, pl. 11, fig. 12–14.

1969 *Phricodothyris asiatica* (Chao): Pavlova, p. 95, pl. 8, fig. 4; pl. 9, fig. 1, 2, textfig. 10–11.

1990 *Phricodothyris asiatica*(Chao): Liang, p. 285, pl. 62, fig. 1–10; pl. 63, fig. 6–11; pl. 65, fig. 18; textfig. 38.

Description.—Average size for genus, moderately ventribiconvex, subcircular to suboval in outline, usually slightly wider than long, especially in early stages; cardinal extremities and lateral and front margins regularly rounded; anterior commissure straight; fold and sulcus absent or very weakly expressed; hingeline approximately half or less than half maximum width; concentric lamellae distinct but not prominent, numbering about seven to eight per five mm near or anterior to midlength.

Ventral valve moderately and evenly convex; beak rather broad, incurved, acute; interarea poorly defined, smooth; delthyrium large, equilaterally triangular, bounded on each side by low stegidial plates that form flanges nearly perpendicular to interarea surface; interior with moderately deep delthyrial ridges and deeply impressed pair of muscle scars.

Dorsal valve slightly less strongly convex than opposite valve; beak broad, blunt, extending into delthyrial opening and partly blocking it; interarea low, relatively narrow, bisected by wide notothyrium; interior not observed.

Measurements.—See Table 21.

Diagnosis.—This species is characterized by its slightly transversely suboval outline, short hingeline, narrow, distinct, concentric lamella, numbering seven or eight per five mm.

Distribution.—*Phricodothyris asiatica* (Chao, 1929) has been found at GSC locality 56430 (five complete specimens and four ventral valves), two complete and one broken shell at GSC locality 56430A, and one almost complete shell from GSC locality C-4085. This species has been described from the Upper Car-

Table 21.—*Measurements (in millimeters) of Phricodothyris asiatica Chao from GSC locality 56430.*

GSC number	Length	Width	Thickness	Hingeline	Width/HL ratio
115662	22.1	22.5	14.2	11.1	2.0
115663	—	21.0	11.8	10.6	2.0
115664	14.0	14.3	9.9	6.7	2.1

→

Fig. 28.—Terebratuloids and retzioids. 28.1–28.20, *Beecheria* cf. *B. itaitubensis* (Derby, 1874), ventral, dorsal, lateral, and anterior views of a growth series of five specimens, GSC 115665–115669, respectively, $\times 1$. 28.21–28.36, *Cranaena nassichuki* n. sp., ventral, dorsal, lateral, and anterior views of four specimens, including the holotype (28.21–28.24), GSC 115670–115673, respectively, $\times 3$. 28.37, 28.38, *Beecheria* sp., ventral and dorsal views of a crushed specimen, GSC 115674, $\times 1.5$. 28.39, 28.40, indeterminate terebratuloid, ventral and anterior views of a ventral valve, GSC 115675, $\times 1.5$. 28.41, *Hustedia* sp., ventral valve, GSC 115676, $\times 3$.

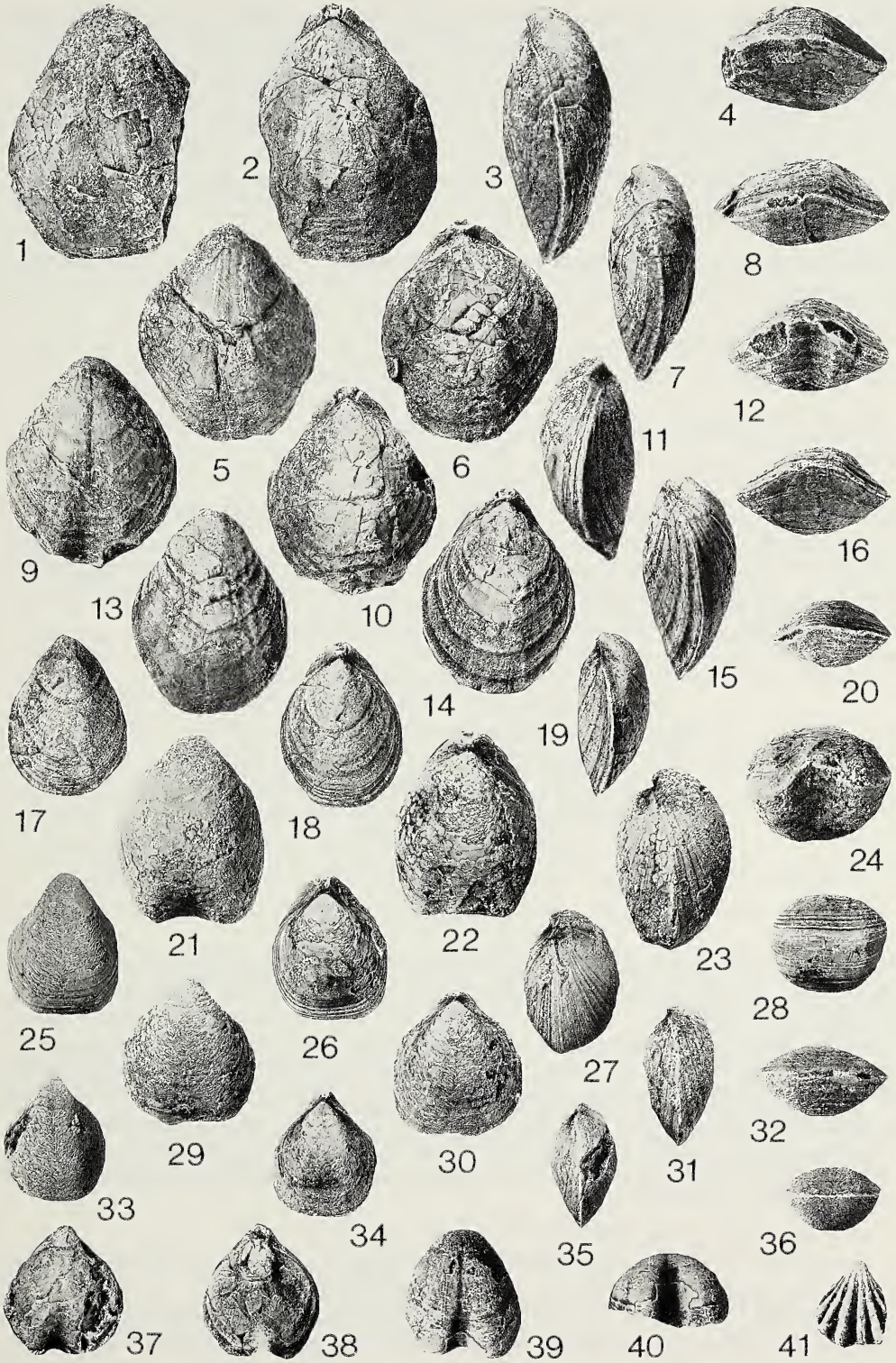


Table 22.—*Measurements (in millimeters) of the types of Cranaena nassichuki, n. sp. from GSC locality 56430.*

GSC number	Length	Width	Thickness
115670	9.1	7.1	5.8
115671	7.0	5.7	4.9
115672	7.1	6.5	3.5
115673	5.9	4.8	3.3

boniferous and Lower Permian of China, Malaysia, Transcaucasus, and the Ural Mountains.

Order Retziidina Boucot, Johnson, and Staton, 1965

Superfamily Retzioidea Waagen, 1883

Family Retziidae Waagen, 1883

Genus *Hustedia* Hall and Clarke, 1893

Hustedia sp.

(Fig. 28.41)

Comments.—A minute ventral valve of a clearly punctate retziid can be assigned to the genus *Hustedia* Hall and Clarke. It bears eight strong subangular costae. A rounded median interspace is present. This specimen falls within the range of morphological variation of several species.

Distribution.—GSC locality 56430 (one ventral valve).

Order Terebratulida Waagen, 1883

Suborder Terebratulidina Waagen, 1883

Superfamily Dielasmatoidea Schuchert, 1913

Family Cranaenidae Cloud, 1942

Genus *Cranaena* Hall and Clarke, 1893

Cranaena nassichuki, **new species**

(Fig. 28.21–28.36)

Holotype.—Figures 28.21–28.24, GSC 115670, from GSC locality 56430.

Paratypes.—Figures 28.25–28.36, three juveniles, GSC 115671–115673, all from GSC locality 56430.

Description.—Small for genus, subequally biconvex; outline rounded subpentagonal to guttate; lateral profile lenticular; anterior profile of large specimens subovate; fold lacking but well-developed sulcus present in anterior third of adult ventral valves; anterior commissure uniplicate in adult shells, rectimarginate in juveniles.

Ventral valve with moderately inflated and narrow umbonal region; lateral slopes evenly convex to lateral margins; sulcus originating well anterior to midlength, rounded, forming emargination in adults in ventral view; beak nearly straight in adults to suberect in juveniles; foramen rounded, epithyridid to mesothyridid; interior with pedicle collar and short dental plates.

Dorsal valve with narrow swollen umbonal region laterally delineated by concave flexures; lateral slopes less convex than those of opposite valve; dorsum well rounded posteriorly, becoming flattened or even slightly concave anteriorly; interior with posteriorly perforate undivided dorsally concave hingeplate; loop not observed.

Measurements.—See Table 22.

Diagnosis.—This species can be differentiated by its well-developed ventral sulcus and moderately narrow ventral umbonal region.

Comments.—Two specimens of this species were sectioned. Although coarsely recrystallized internally, enough internal details were gleaned from these speci-

mens to suggest that this species is most likely a *Cranaena*, although the loop was not preserved in either specimen. *Cranaena* is rare above the Lower Carboniferous with species being described by Lane (1962) from the Lower Moscovian of Nevada, Czarniecki (1969) from the Gzhelian of Spitsbergen, and Kallashnikov (1980) from the Bashkirian of Novaya Zemlya and the Asselian of the northern Urals. None of these species is closely similar externally to this Hare Fiord species, all having somewhat broader ventral umbones and thicker profiles.

Distribution.—GSC locality 56430 (13 specimens, two sectioned).

Family Heterelasminidae Likharev, 1956

Genus *Beecheria* Hall and Clarke, 1893

Beecheria cf. *B. itaitubensis* (Derby, 1874)

(Fig. 28.1–28.20)

1874 *Terebratulula itaitubensis* Derby, p. 1, pl. 2, fig. 1, 3, 8, 16; pl. 3, fig. 24; pl. 6, fig. 15.

Description.—Large, subequally biconvex, moderately compressed, much longer than wide; outline longitudinally guttate to rounded subquadrate; lateral and anterior profiles lenticular; maximum width varying from just in front of midlength to just posterior to it; venter flattened or with shallow sulcus; dorsum in anterior profile arched to evenly rounded; anterior commissure weakly uniplicate to rectimarginate; surfaces smooth except for irregularly spaced growth varices and faint fine growth lines.

Ventral valve with moderately elongated umbonal region; lateral slopes and venter evenly and moderately convex; sulcus, if present, very weak and shallow, confined to anterior half of valve; beak ridges rounded but well differentiated; beak nearly erect; foramen large, subovate, permesothyridd; deltidial plates not observed, obscured by beak; interior with strong short dental plates.

Dorsal valve moderately inflated, less convex than opposite valve, most convex posteriorly, with moderately to prominently arched dorsum in large specimens, more evenly convex in juveniles; lateral slopes gently convex; beak acute, small, obscured by ventral valve; interior with inner and outer hingeplates sessile and forming tent-like structures, fused medially with valve floor and forming false median septum, bearing crural bases at peaks.

Comments.—This species is similar in outline and size to *Beecheria itaitubensis* Derby from the Desmoinesian of the Amazon Basin, Brazil. Mendes (1957) illustrated a small specimen of this species with similar outline and appearance from the same general horizon and region as Derby's specimens.

Distribution.—GSC locality 60194 (36 specimens).

Beecheria sp.

(Fig. 28.37, 28.38)

Comments.—This small, crushed specimen bears the two tent-like structures on the floor of the dorsal valve that characterize the genus *Beecheria*. A narrow ventral umbonal region and strong foldsulcus preclude a close relationship with the species described above as *Beecheria* cf. *B. itaitubensis* (Derby). The modest size and strong foldsulcus of this specimen suggest similarity to *Beecheria daltonensis* Sutherland and Harlow, 1973, from Moscovian-age beds in New Mexico. Most illustrated specimens of the latter have a broader ventral umbonal region and a robust lateral profile, a feature not ascertainable in this crushed specimen.

Distribution.—A single, crushed specimen from GSC locality C-5202.

Indeterminate terebratuloid

(Fig. 28.39, 28.40)

Comments.—This disarticulated ventral valve is similar in size to the specimen described above as *Beecheria* sp. It has a well-developed sulcus like that specimen

but the ventral umbo is broad and well rounded laterally. This specimen is not crushed but lacking a dorsal valve cannot be assigned to a genus.

Distribution.—A single ventral valve from GSC locality C-5202.

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TAXONOMIC STATUS OF THE EARLY PERMIAN *HELODECTES*
PARIDENS COPE (DIADECTIDAE) WITH DISCUSSION OF
OCCLUSION OF DIADECTID MARGINAL DENTITIONS

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ABSTRACT

Helodectes paridens Cope (1880) is a problematic Early Permian taxon from Texas that has been considered variously as a diadectid or captorhinid, or simply indeterminate. It was based on a poorly preserved jaw and adjoining elements of the left side of a small skull that was believed to possess a double row of marginal teeth. Thorough preparation of the holotype reveals that one row represents a normal complement of rooted premaxillary and maxillary teeth and the other a row of crowns derived from the opposing teeth of the absent dentary. There are no detectable differences from the commonly encountered *Diadectes* of the same age, and *Helodectes* should be regarded as a junior synonym of that genus. As the holotype of *H. paridens* exhibits no features on which to base specific identity, it is referred to as *Diadectes* sp. The same interpretation undoubtedly applies to the double row of premaxillary-maxillary marginal teeth in the lost and only known specimen of the equally small holotype of *H. isaaci* Cope (1880) from the same locality as *H. paridens*. A second example of *Helodectes*-like dental preservation is described in the opposing upper and lower jaw elements in a very small *Diadectes* specimen from the Early Permian of Texas.

The double-toothed row preservation of the marginal teeth in these specimens prompts discussion of aspects of the occlusion of the cheek teeth in *Diadectes* and those in the closely related Late Pennsylvanian *Desmatodon*. It is speculated that, in addition to occlusion between the upper and lower cheek teeth, mastication also occurred through contact between the maxillary cheek teeth and the inner surface of the parapet of the dentary, and between the cheek teeth of the dentary and the ventral surface of the secondary palatal shelf of the palatine. Changes in the pattern of attrition indicate that with increased molarization the occlusion between the upper and lower cheek teeth shifted from a strictly side-to-side contact in extremely small juveniles to a strictly dorsoventral, vertical-alignment contact between the upper surfaces of the crowns in adults. In the adult pattern of occlusion the upper and lower cheek-tooth series were only partially aligned dorsoventrally, and it is assumed that the labial margin of the upper series and the lingual margin of the lower series occluded with the inner surface of the dentary parapet and the ventral surface of the secondary palatal shelf of the palatine, respectively. These changes in the molarization and occlusion from extremely small juveniles to adults may have been accompanied by a shift in diet.

KEY WORDS: Diadectidae (*Diadectes*), *Helodectes*, dentition, Early Permian

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INTRODUCTION

Olson's (1947) study of the family Diadectidae was initiated with the aim of 1) better understanding the Cotylosauria, then considered by most to include all the primitive reptiles lacking temporal openings and comprising the Diadectomorpha, Captorhinomorpha, and Seymouriamorpha; and 2) a revision of the classification of the Reptilia, now considered as a paraphyletic grouping. The diadectomorph family Diadectidae was considered by him as occupying a central position to these two endeavors, because it is the family on which Cotylosauria was founded and because of the availability of specimens of its member genera, particularly the type genus *Diadectes*, that permitted detailed anatomical study. Upon examination of most of the existing diadectid materials collected from the Late Pennsylvanian and Early Permian of North America, Olson (1947) concluded that of the then 11 recognized genera only *Diadectes* Cope, 1878, *Desmatodon* Case, 1908, and *Diasparactus* Case, 1910, are valid taxa. Subsequent studies of new and more complete specimens of the poorly known *Desmatodon* have strongly reaffirmed the validity of this taxon (Vaughn, 1969, 1972; Berman and Sumida, 1995). Seven of the diadectid genera (*Empedocles* Cope, 1878, *Nothodon* Marsh, 1878, *Chilonyx* Cope, 1883, *Empedias* Cope, 1883, *Bolbodon* Cope, 1896, *Diadectoides* Case, 1911, and *Animasaurus* Case and Williston, 1912) were reevaluated by Olson (1947) as synonymous with *Diadectes*. He concluded that the specimens on which these genera were based either exhibited no features that could be used to differentiate them from *Diadectes* or exhibited features which are highly variable with age, such as thickness and rugosity of cranial bones or proportional differences in skeletal elements, and therefore could not be considered to be of generic, or even specific, significance.

The remaining genus to be considered and the subject of this report is *Helodectes*, which was originally described and referred to the Diadectidae by Cope (1880). Cope (1880:48-49) described *Helodectes* as represented by two species, each based on a single specimen of jaw fragment with teeth and collected presumably from the same Early Permian, Wichita Group, site in Texas by Jacob Boll between 1878 and 1880 (Romer, 1958). The specimen on which was founded the first named species, *H. paridens*, was described by Cope as a left maxilla and probable adjoining premaxilla (AMNH 4346). The jaw fragment was very poorly preserved and encrusted with a very incalcitrant, oxidized iron matrix. Most unusual and forming the basis of Cope's (1880) generic diagnosis was the presence of both an inner and outer row of marginal teeth. The second species of *Helodectes* described by Cope, *H. isaaci*, was based on a probable fragment of maxilla also possessing a double row of teeth (catalogue number not given) and exhibiting the same poor quality of preservation. According to Case (1911), the holotype and only known specimen of *H. isaaci* is lost and no specimen can be identified from Cope's description. The two *Helodectes* species were distinguished from one another by the number, relative sizes, and arrangements of the teeth. Cope (1880) noted that occurring with the type specimens of both species of *Helodectes* were diadectid skeletal fragments that could belong to either of them or even to a small specimen of *Empedocles*, whose teeth were included in the same lot. These materials were not described, however, because of the uncertainty of association. Case (1911:48) believed it was very doubtful that additional specimens of *Helodectes* could be identified with confidence because of the poor quality of the holotypic material. Continuing, he remarked that the "numerous teeth in the frag-

ment of the jaw indicate a member of the suborder Pareiasauria, but that the fragment and the roots of the teeth indicate an animal much larger than any well-known member of the suborder.” For these reasons he retained the genus provisionally as a captorhinid. In Olson’s (1947) opinion, however, the unassigned skeletal fragments found with the holotype of *H. paridens* are so poorly preserved that only some of the postcranial fragments can be very doubtfully referred to Diadectidae. He, therefore, concluded that the jaw fragment of *H. paridens* does not belong to this group, and, although some of the associated postcranial fragments are diadectid, the genus must be rejected as indeterminate.

Preparation of the holotype of *Helodectes paridens* reveals that it possesses only a single row of rooted, premaxillary–maxillary teeth lacking their crowns. The second row of teeth observed by Cope (1880) consists of the crowns of the dentary dentition of the opposing lower jaw that has been lost due to weathering. Peter P. Vaughn of the University of California, Los Angeles, realized the true nature and origin of the dentition of *Helodectes* as early as the mid-1960s. One of us (DSB), while a graduate student of Vaughn, recalls having been told by him the explanation for the double row of teeth in *Helodectes*. His evidence was almost certainly based initially on an at-hand collection of undescribed jaw and postcranial elements of several extremely small individuals of *Diadectes* from the Early Permian of Texas (collectively catalogued as MCZ 2780). Included was a set of upper and lower jaw elements that not only exhibits the identical, double-toothed row condition seen in the holotype of *H. paridens*, but when rejoined in their original, preserved position also reveals clearly the origin of the deceptive appearance of its dentition. He later confirmed his suspicion by examining the holotype of *H. paridens*. It was not until the loan of the MCZ 2780 material was transferred to the Carnegie Museum of Natural History that the authors became aware of the *Helodectes*-like set of jaws and realized its implications. Careful examination of the holotype of *H. paridens* not only resolves the riddle of its dentition, but also provides indisputable evidence that it should be assigned to Diadectidae as *Diadectes*, although a species assignment cannot be made safely. Presumably the same conclusions would apply to the missing holotype of *H. isaaci*.

The double-toothed row preservation has prompted a reconsideration of the function of the secondary palatal shelf of the palatine and the parapet of the dentary as providing masticatory surfaces for the lower and upper cheek teeth, respectively, in *Diadectes* and the closely related Late Pennsylvanian *Desmatodon*. In addition, pronounced changes in the molarization and occlusion of their cheek teeth from extremely small juveniles to adults may have been accompanied by a shift in diet.

The following abbreviations are used throughout the text to refer to repositories of specimens: AMNH, American Museum of Natural History, New York, New York; CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.

DESCRIPTION OF *HELODECTES PARIDENS*, HOLOTYPE, AMNH 4346

The holotype and only known specimen of *Helodectes paridens*, AMNH 4346, consists not only of the articulated left premaxilla and maxilla, as originally described by Cope (1880), but also portions of the adjoining lacrimal, jugal, palatine,

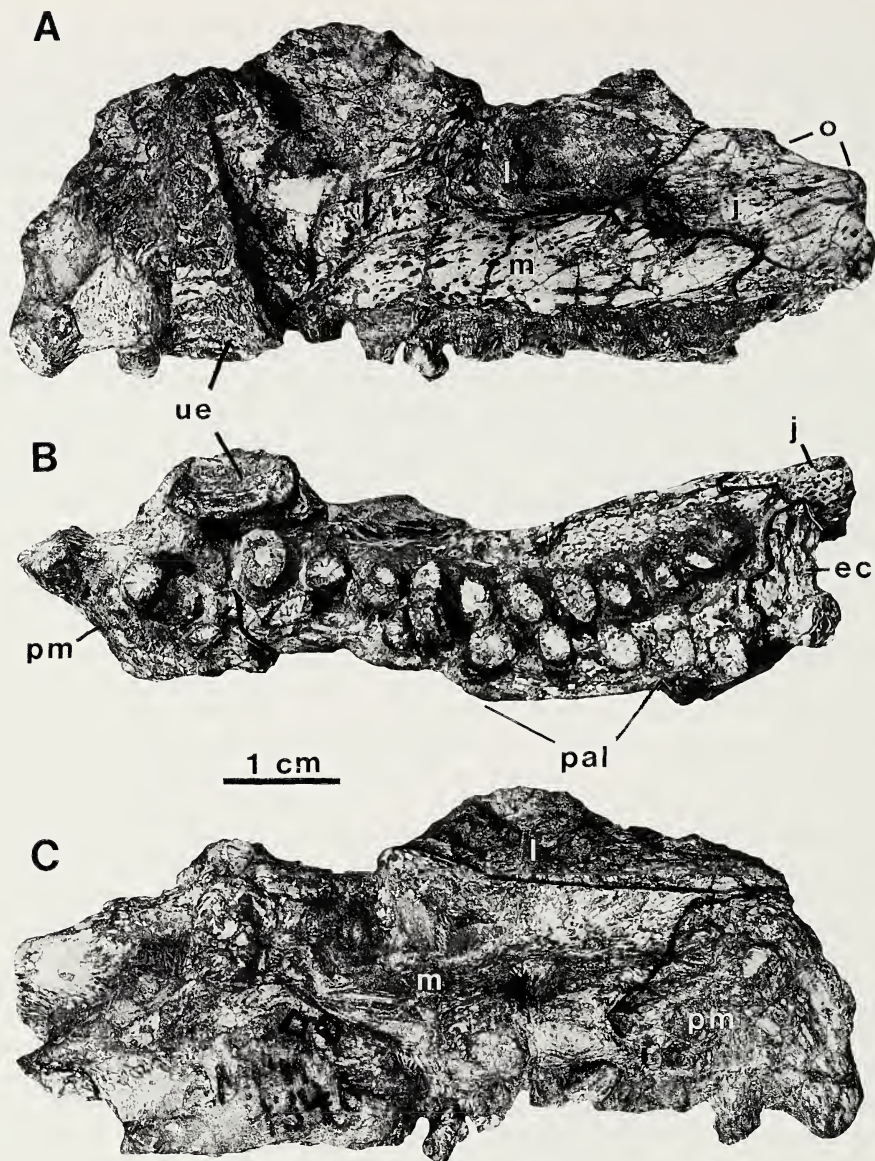


Fig. 1.—*Diadectes* sp. (AMNH 4346), holotype of *Helodectes paridens*, consisting of upper left jaw and portions of adjoining elements. A, lateral (anterior to left); B, occlusal; and C, medial (anterior to right) views. Abbreviations: ec, ectopterygoid; j, jugal; l, lacrimal; m, maxilla; o, orbital rim; pal, secondary palatal shelf of the palatine; pm, premaxilla; ue, unidentified element.

and ectopterygoid (Fig. 1, 2). The holotype is mediolaterally crushed dorsal to the alveolar shelf, and a large, unidentified fragment of bone adheres to its lateral surface at the premaxillary-maxillary union. The premaxilla lacks the dorsal process and, as explained below, probably a small portion of its anterior, symphyseal region that included the anteriormost tooth. There is seemingly very little missing

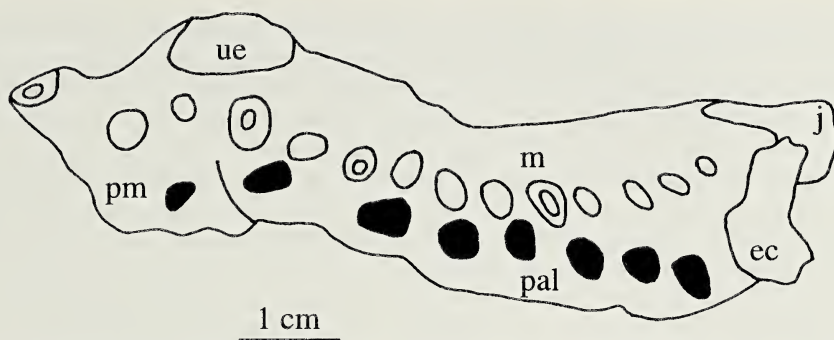


Fig. 2.—*Diadectes* sp. (AMNH 4346), holotype of *Helodectes paridens*. Outline drawing of Figure 1B to identify marginal dentitions of upper and lower jaws. Incomplete teeth shown as cross-sectional outlines drawn at level in which preservation ends. Ankylosed premaxillary–maxillary tooth bases shown as open outlines and isolated dentary tooth crowns as filled-in outlines. Abbreviations as in Figure 1.

from the maxilla except for the crowns of its teeth, although poor preservation makes it impossible to define all of its borders.

The marginal dentition is undoubtedly the most important and interesting aspect of AMNH 4346. Cope's (1880) original description of the holotype of *Helodectes paridens* (AMNH 4346) focused on what he believed to be its unique possession of two rows of marginal teeth. It is now quite apparent that the outer or lateral row, consisting of 14 teeth, is the only series of teeth ankylosed to the premaxilla and maxilla. All that remains of this series of teeth are the bases. Those of the first three teeth are subcircular in horizontal section and decrease serially in size posteriorly, with the third being markedly smaller than the two preceding it. The base of the fourth tooth is equal to the first in basal diameter and has a slightly transverse, oval outline, whereas the fifth tooth base is considerably smaller than the fourth and circular in outline. The bases of the succeeding teeth gradually increase in size, particularly in becoming transversely oval, to the tenth, whereas those of the last four teeth, which are noticeably the smallest of the entire series, gradually decrease serially in size posteriorly. In occlusal view the premaxillary–maxillary tooth row forms a slightly sigmoidal curve, with the anterior half of the series forming a labially convex curve and the posterior half forming a lingually convex curve. The bases of the oval, midseries cheek teeth are not oriented directly transversely, as the labial edges are slightly in advance of the lingual edges. Although the premaxillary–maxillary suture cannot be traced across the entire alveolar surface, it probably passed between the third and fourth preserved tooth bases. This determination is based in part on the fact that in *Diadectes* jaws examined by us, the last premaxillary tooth is typically much smaller than the preceding teeth of the premaxilla and the first tooth of the maxilla. Because the premaxilla of North American *Diadectes* possesses four teeth, it is also reasoned that the first tooth and the symphyseal portion of the premaxilla surrounding it have been lost. If this analysis is correct, the total tooth count for the upper jaw is four premaxillary and 11 maxillary teeth, which is the standard count for *Diadectes*.

Medial to the premaxillary–maxillary tooth row is a row of eight teeth, or more accurately their crowns, that undoubtedly represents a portion of the marginal

series of the opposing dentary of the lower jaw. Although the two series lie closely adjacent to one another for most of their length anteriorly, they diverge posteriorly. The size relationships of the dentary teeth to each other can only be approximated because of poor preservation and the separation of the crowns from their bases at various levels. The anteriormost two tooth crowns lie adjacent to the third and fourth tooth bases of the upper jaw series, with the first being much smaller than the second in cross-sectional size. The succeeding six tooth crowns of the dentary dentition are closely spaced without gaps and, except for the first crown, are preserved adhering to the ventral surface of the palatine between the levels of the seventh and 14th tooth bases of the premaxillary-maxillary series. The posteriormost four crowns are subequal in cross-sectional size and somewhat expanded transversely, with the labial edge of each lying slightly in advance of the lingual edge. Whereas the two crowns preceding the posteriormost four are substantially larger, their margins are too incomplete to determine outline shape. Very little information about the morphology of the crowns is available, because they are closely attached to the bone of the upper jaw and palate and are too closely spaced to prepare fully. The second and fourth crowns are roughly single, conical cusps and are considerably longer than those of the succeeding dentary teeth. All that can be said of the remaining crowns is that those of the fifth and sixth are low and moderately expanded transversely, without any obvious appearance of medial or lateral cusps. The cross-sectional exposures of the teeth of both rows reveal a labyrinthine structure.

By way of comparison with North American *Diadectes* dentitions and considering the spatial relationships of the dentary crowns to the premaxillary-maxillary teeth, the first and second dentary crowns in AMNH 4346 likely represent the third and fifth tooth positions of the complete series. Continuing, if the gap following the second preserved tooth crown is considered equivalent to two teeth, then the remaining six posteriormost crowns represent the eighth through 13th tooth positions of the complete series. If this analysis is correct, then probably somewhere between one and five posteriormost dentary teeth are not represented, as, according to Welles (1941), the number of lower jaw teeth in *Diadectes lentus* from the Early Permian Wichita Group of Texas varies from 14 to 18. However, because the dentaries of small or juvenile specimens of *Diadectes* generally contain fewer teeth than those of adults, it is suspected that the number in AMNH 4346 was probably 14 or possibly 15. As an example, in the skull of the small, immature specimen *Diadectes sanmiguelensis* MCZ 2989 from the Lower Permian Cutler Formation of Colorado (Lewis and Vaughn, 1965), the dentary possesses a total of 14 teeth.

A small, badly weathered portion of the lacrimal remains articulated with the dorsal lamina of the maxilla, but the union is visible only on the medial surface of AMNH 4346. Only the anterior end of the jugal, where it contacts the maxilla along the jaw margin, is preserved and includes, as Cope (1880) noted, a small portion of its entrance into the orbital rim. The incomplete palatine is represented mainly by a narrow, arcuate shelf of bone that extends ventromedially from its contact with the inner margin of the maxillary alveolar shelf. This portion of the palatine is referred to as the secondary palatal shelf by Olson (1947) and Berman and Sumida (1995), and, although its suture with the maxilla cannot be discerned, it is most easily located in AMNH 4346 by the row of six tooth crowns of the dentary adhering to its ventral surface. Undoubtedly, the complete palatine of AMNH 4346 was identical to those in North American and German *Diadectes*

and *Desmatodon* (Olson, 1947; Berman and Sumida, 1995; Berman et al., 1998) in which a primary palatal shelf of the palatine (absent here), lying a short distance dorsal to the secondary palatal shelf, extended medially to contact the pterygoid as part of the true palate. A portion of the otherwise small ectopterygoid contacts the posterior margin of the secondary palatal shelf of the palatine, the posterior end of the alveolar shelf of the maxilla, and the anterior ventral margin of the medial surface of the jugal. This portion of the ectopterygoid forms a very short continuation of the secondary palatal shelf of the palatine and the anterior medial border of the subtemporal fenestra, which when complete would have contacted the distal end of the anterior margin of the transverse flange of the pterygoid. Olson's (1947:fig. 3) reconstruction of the skull of *Diadectes* in ventral view clearly depicts these structural relationships of the ectopterygoid, although the jugal is mislabeled as the squamosal.

A SECOND EXAMPLE OF *HELODECTES*-LIKE DENTAL PRESERVATION

A pair of opposing upper and lower, left jaw elements (Fig. 3), belonging to a single *Diadectes* specimen, provides indisputable evidence for the above interpretation of the double row of marginal teeth in the holotype of *Helodectes paridens*. Both jaw fragments are part of a large collection of undescribed, isolated, tooth-bearing jaw and mainly disarticulated postcranial elements representing at least three extremely small juveniles of *Diadectes* from the Lower Permian Wichita Group of Texas that were collectively catalogued as MCZ 2780 without specific assignment. For the purpose of description, however, the two jaw fragments which are the focus here have been recatalogued as MCZ 9331. They not only duplicate the double-toothed row condition in AMNH 4346, but most importantly can be rejoined in their original, preserved position to demonstrate that one of the two rows of teeth in each jaw represents the crowns of the opposing jaw dentition.

The upper left jaw fragment of MCZ 9331 (Fig. 3) includes essentially the entire maxilla, a small portion of the jugal that extends between its contact with the posterior dorsal margin of the maxilla and the anteroventral rim of the orbit, most of the lacrimal, and at least the greater portion of the secondary palatal shelf of the palatine. Although a series of 12 maxillary teeth is represented (Fig. 3C, 4A), the first and last teeth are represented by empty alveoli, teeth 2 through 4 and 6 through 9 are variably incomplete, teeth 5 and 10 are partially erupted crowns, and only tooth 11 is essentially complete. All of the teeth except possibly the last two appear to exhibit some transverse expansion, with those of the mid-series region being the most expanded. The crown of a replacement tooth is visible in the lingual pit of the third tooth. It is possible that the partial alveolus at the anterior end of the maxilla actually held the posteriormost premaxillary tooth, as the maxilla of *Diadectes* typically possesses 11 teeth. Although poor preservation makes it difficult to describe serial size changes in the maxillary teeth, some general remarks are possible. On the basis of their basal diameters, the anteriormost and largest teeth of the series decrease serially in size posteriorly to about the fifth tooth, the succeeding three teeth are subequal, and the last four teeth exhibit a noticeable serial decrease in size posteriorly. Lying medially adjacent to maxillary teeth 7 through 11 and adhering to the ventral surface of the secondary palatal shelf of the palatine is a series of four, closely spaced crowns belonging to teeth 7 through 10 of the marginal dentition of the opposing lower jaw dentary.

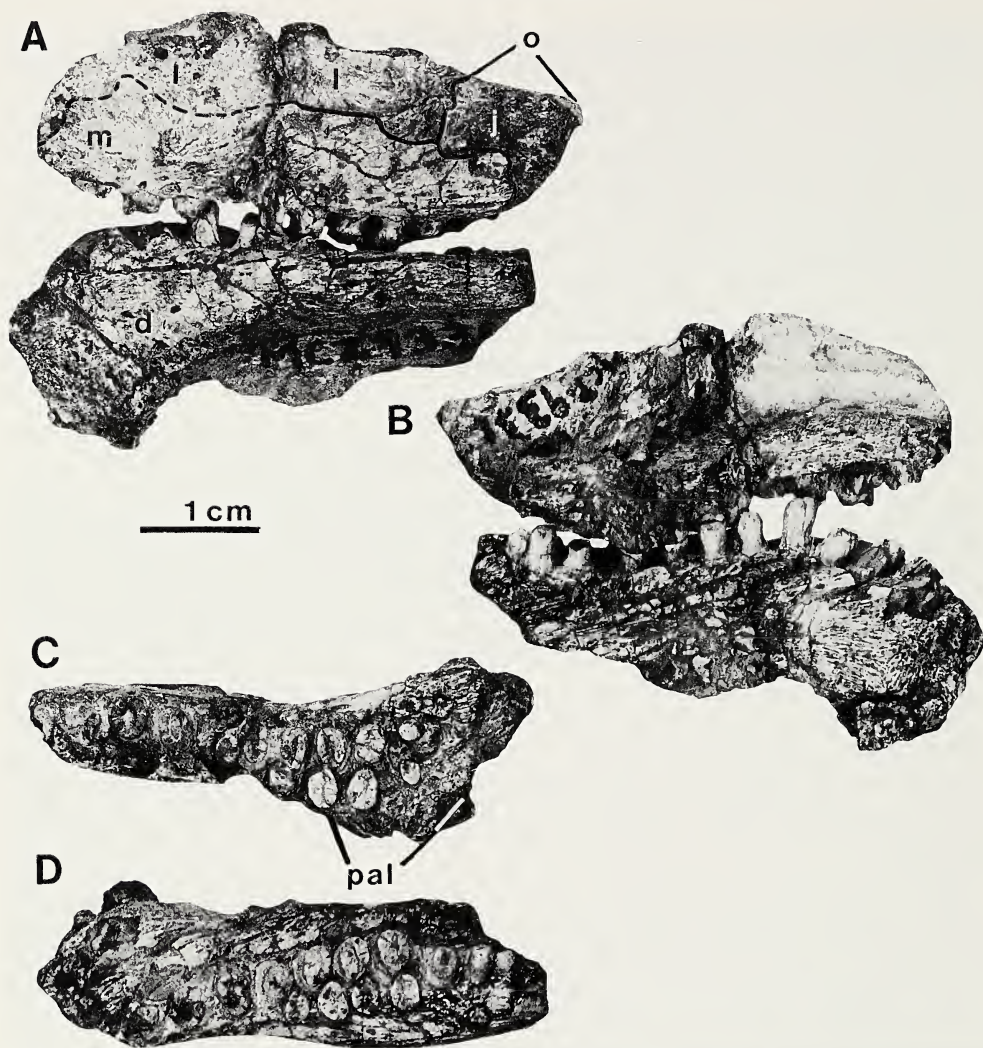


Fig. 3.—*Diadectes* sp. (MCZ 9331). A, lateral, and B, medial views of upper and lower jaw fragments joined in original preserved position. C and D, upper and lower jaw fragments, respectively, in occlusal (anterior to left) view. Abbreviations: d, dentary; j, jugal; l, lacrimal; m, maxilla; o, orbital rim; pal, secondary palatal shelf of the palatine.

Serial identifications of the separated dentary tooth crowns, as well as those of the maxilla adhering to the dentary discussed below, are easily determined, as the two jaws can be rejoined so that all the crowns except that of the 12th maxillary tooth contact in an exact union the tooth bases of their origin.

The lower jaw fragment of MCZ 9331 (Fig. 3) includes only the dentary, which appears to be missing mainly a small portion of its posterior end. A continuous row of 12 tooth bases extends the length of the alveolar shelf (Fig. 3D, 4B). As the small margin of the shelf posterior to the last tooth does not exhibit any signs of additional teeth, the entire marginal series of the dentary may be represented. Typically, however, the dentary of *Diadectes* held at least 14 teeth. Using basal

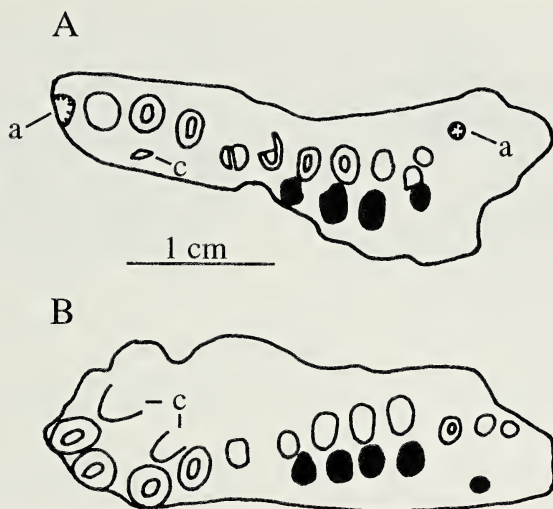


Fig. 4.—*Diadectes* sp. (MCZ 9331). Outline drawings of Figure 3C and D to indicate marginal dentitions of upper and lower jaws. Ankylosed maxillary and dentary tooth bases of A and B, respectively, shown as open outlines and separated dentary and maxillary tooth crowns of A and B, respectively, shown as filled-in outlines. Abbreviations: a, empty alveolus; c, crown of replacement tooth.

diameter as an indication of size, in general the first five teeth, which included the largest of the series, decrease serially in size posteriorly, the succeeding four teeth are noticeably smaller and exhibit a modest serial increase in size posteriorly, and the last three teeth, the smallest of the series, decrease serially in size posteriorly. The anterodorsal inclination of the first four tooth bases indicates that these teeth were procumbent as in *Diadectes*. The crowns of replacement teeth in the lingual pits of the first and third teeth also indicate that the first four teeth were *Diadectes*-like in being bluntly spatulate and incisiform. Lying immediately lateral to teeth 6 through 9 is a series of four closely spaced crowns belonging to teeth 6 through 9 of the marginal dentition of the opposing upper jaw maxilla. Following a small gap, a fifth crown belonging to the 12th maxillary tooth lies a short distance labial to dentary tooth 11.

DISCUSSION

Taxonomic Status of Helodectes

Restudy of the Early Permian holotype of *Helodectes paridens* AMNH 4346 clearly indicates that it should be regarded as a junior synonym of *Diadectes* of the same age. The poorly preserved bones of the left side of the skull that comprise AMNH 4346 deviate in no recognizable way from those in *Diadectes*. Most noteworthy, the unusual structure of the palatine, specifically the presence of the secondary palatal shelf, is known elsewhere only in *Diadectes* and the very closely related Late Pennsylvanian *Desmatodon* (Olson, 1947; Berman and Sumida, 1995). The extremely small size of AMNH 4346, as well as the *Diadectes* specimens MCZ 2780 and 9331, represents an early ontogenetic stage of growth seldom encountered and rarely described in this genus (Olson, 1947; Lewis and Vaughn, 1965; Berman and Sumida, 1995). Small size combined with concomitant differences in skeletal proportions and dental features from those of adult

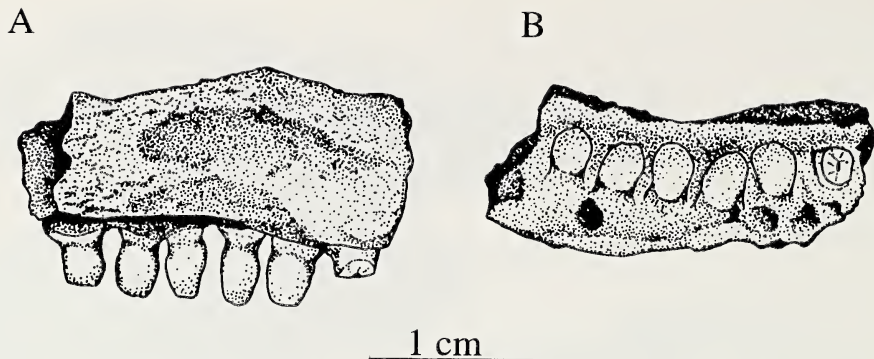


Fig. 5.—*Diadectes* sp. (MCZ 2780). A, lateral, and B, occlusal views of partial right juvenile maxilla.

specimens undoubtedly misled, as Olson (1947) noted, early investigators to interpret juvenile specimens of *Diadectes* as pertaining to other genera. This confusion was partly resolved, however, with the recent description (Berman and Sumida, 1995) of the prominent, ontogenetic changes in the marginal dentition of *Diadectes*. That study clearly accounts for the differences between the dentition of AMNH 4346 and those of adult specimens of *Diadectes* as reflecting widely separated, ontogenetic growth stages. The dentition of juvenile specimens of *Diadectes*, including AMNH 4346, can be most easily distinguished from that of adults by the cheek teeth. In contrast to adults, the cheek teeth in juveniles do not exhibit extreme transverse expansion and molarization that results in the central cusp being flanked lingually and labially by a lower, but prominent, shoulder-like cusp. In order to emphasize this observation, Berman and Sumida (1995) stated that the maxillary and dentary cheek teeth in the very immature specimens of *Diadectes* MCZ 2780 (including MCZ 9331) and *D. sanmiguelensis* MCZ 2989 exhibit little transverse widening, and are more accurately described as bulbous, with a weakly developed central cusp and essentially no lingual or labial shoulder-like cusps (Fig. 5). Despite representing an early juvenile stage of development, the dentition of AMNH 4346 is still like that of adult specimens of *Diadectes* in duplicating in greater or lesser degree numerous features of the teeth, such as their number, arrangement, morphology, and serial changes (Case, 1911; Lewis and Vaughn, 1965; Berman and Sumida, 1995).

AMNH 4346 might be suspected of being a juvenile specimen of the rare, Late Pennsylvanian *Desmatodon*, whose cranial anatomy, including its dentition, is nearly identical to that of the later-occurring *Diadectes* (Vaughn, 1972; Berman and Sumida, 1995). The potential for this confusion, however, is confidently eliminated by considering the subtle differences in the juvenile dentitions of these two genera first noted by Vaughn (1972) and later more fully documented by Berman and Sumida (1995). They list four dental features of the juvenile maxilla in *Desmatodon* which are absent or greatly reduced in mature specimens of this genus and apparently not present in specimens of *Diadectes* of any age: 1) fewer number of teeth, 2) greater relative spacing of teeth, 3) first two maxillary teeth relatively longer and more incisiform, and 4) absence of wear facets. Features 1 and 2 clearly identify AMNH 4346 as *Diadectes*, whereas poor preservation prevents the use of features 3 and 4.

Specific assignment of AMNH 4346 and MCZ 2780 and 9331 is impossible

on morphological grounds. However, if one were to follow the recommendations in Olson's (1947) study of the systematics of Diadectidae, tentative assignment to *Diadectes sideropelicus* could be suggested on stratigraphic grounds, as it is the only species that he recommended be recognized from the Wichita beds of Texas until such evidence to the contrary is described.

Occlusion of Diadectid Marginal Dentitions

On the basis of not only dental anatomy, but also features of the entire skeleton, the diadectids *Desmatodon* and *Diadectes* were interpreted by Hotton et al. (1997) as the earliest known examples of vertebrates having a primarily high-fiber diet of terrestrial plants. It is, of course, the unusual features of their dentitions which have provided the most persuasive arguments for considering them as herbivores. The anterior, procumbent, rather spatulate, incisiform teeth are ideally suited for grasping and cropping vegetation, whereas the uniquely molariform cheek teeth are indicative of a highly specialized masticatory structure for dealing with a tough, high-fiber plant diet. Wear patterns confirm a vertical motion of the anterior incisiform teeth and a backward or propalinal motion of the lower jaw cheek teeth against those of the upper jaw during occlusion and mastication (Hotton et al., 1997).

The unusual preservation of the dentitions of AMNH 4346 and MCZ 9331 prompts speculation of other aspects of the occlusion of the cheek teeth in *Diadectes* and *Desmatodon*. In the extremely small marginal dentitions of AMNH 4346 and MCZ 2780 and 9331 most of the crown tips of the cheek teeth are either not exposed or are too poorly preserved to reveal wear facets. In a few instances, however, the crowns in MCZ 2780 are exposed and preserved well enough to note that attrition is either absent or limited to small, subcircular facets on the lingual and labial surfaces of the upper and lower cheek teeth, respectively. The pattern of wear is greatly restricted, despite the cheek teeth being bulbous to moderately expanded transversely, and could have been achieved only if occlusion was restricted to contact between the labial surfaces of the lower and the lingual surfaces of the upper cheek teeth during propalinal movement of the lower jaw. The absence of attrition on the tips of the crowns, however, does not necessarily indicate that they did not participate directly in the mastication of food. To the contrary, there are several features of AMNH 4346 and MCZ 9331 which suggest strongly an additional, occlusal component of the cheek teeth that involves the crown tips. The most persuasive feature is the side-by-side preservation of their upper and lower dentitions, with the crown tips of the dentary cheek teeth contacting the ventral surface of the secondary palatal shelf of the palatine and the crown tips of the maxillary cheek teeth contacting the dentary lateral to its dentition. If considered in combination with the limited attrition pattern of the cheek teeth, then it seems very plausible that the above associations of the crown tips of the dentary and maxillary cheek teeth with the palatine and dentary, respectively, indicate an additional, important masticatory component of the cheek teeth. Additionally, in AMNH 4346 and MCZ 9331 the secondary palatal shelf of the palatine curves strongly ventromedially, creating a channel-like space between it and the lingual surfaces of the maxillary cheek teeth. Therefore, it is very likely that the lingual margins, as well as the crown tips, of the cheek teeth of the maxilla contacted the secondary palatal shelf during mastication.

If occlusion of the dentary cheek teeth with the palatine is accepted, it forces

a reconsideration of previous interpretations of the functional role of the secondary palatal shelf of the palatine. Commenting on this unique structure in *Diadectes*, now known to occur also in *Desmatodon* (Berman and Sumida, 1995), Olson (1947:16) noted that the "ventral surface of the process is rough and there usually are a few small teeth along its posterior margin. This has been the basis for considering its primary function as masticatory" by earlier authors. Olson was convinced, however, that the secondary palatal shelf more probably represents the incipient development of a secondary palate. Crucial to the interpretation of this structure is an excellently preserved, isolated palatine of *Desmatodon* (CM 47674) described in detail and as identical to that in *Diadectes* by Berman and Sumida (1995). The ventral surface of the secondary palatal shelf was characterized (Berman and Sumida, 1995:322-323) as "distinctly sculptured by short, shallow, irregular channels and low ridges, and a few, scattered, minute tubercular prominences." The coarse sculpturing of the secondary palatal shelf suggests the presence of a tough, perhaps keratinized, tissue covering. This would have provided an ideal masticatory surface for the dentary cheek teeth. Also pertinent to this discussion is the description (Berman and Sumida, 1995) of a shagreen of denticles distributed over areas of the posterior portion of the channel formed between the primary and secondary palatal shelves of the palatine in *Desmatodon*. This was interpreted as contradictory evidence of Olson's (1947) theory that the secondary palatal shelf represents a partially developed secondary palate.

A twofold, occlusal pattern of the maxillary cheek teeth during mastication, similar to that suggested for the dentary cheek teeth, can also be hypothesized. In specimens of *Diadectes* and *Desmatodon* having complete dentaries there exists an unusual, unique structure that suggests the possible presence of a specialized masticatory surface. Lateral to the bases of the cheek teeth is a shallow groove whose outer wall is formed by a vertical extension of the lateral surface of the dentary into a thin, flange-like ridge or parapet (Welles, 1941; Vaughn, 1972; Berman and Sumida, 1995). Welles (1941:424) remarked that "this flange resembles that of the *Chelonia* and *Anomodontia* and could very well have served a similar purpose; that is, to support a horny cutting beak." This interpretation, however, is susceptible to the observation that the outer surface of the parapet exhibits the same coarse surface sculpturing that occurs over the entire lateral surface of the lower jaw. That is, there is no distinct change in the bone texture along the outer jaw margin to support the presence of a horny beak, although this does not preclude a cropping function of the parapet. More important to the discussion here, however, is the channel-like basin formed between the parapet and the cheek teeth, as it approximates the occlusal position of the crown-tips and labial margins of the maxillary cheek teeth. Therefore, the parapet of the dentary not only closely duplicates that of the secondary palatal shelf of the palatine in structure, but probably also functioned as a masticatory surface. The internal surface of the parapet, which also forms the outer margin of the floor of the channel-like basin, is coarsely sculptured in a manner very similar to that of the secondary palatal shelf of the palatine and conceivably could have been covered also by a tough, keratinized tissue. In this connection, it is suspected that both the crown tips and labial margins of the maxillary cheek teeth contacted the inner surface of the parapet and channel during mastication. Although incomplete preservation prevents identification of a parapet and groove lateral to the dentary cheek teeth in the juvenile specimens MCZ 2780 and 9331, these structures are present in *D. sanmiguelensis* MCZ 2989 (Lewis and Vaughn, 1965) which is

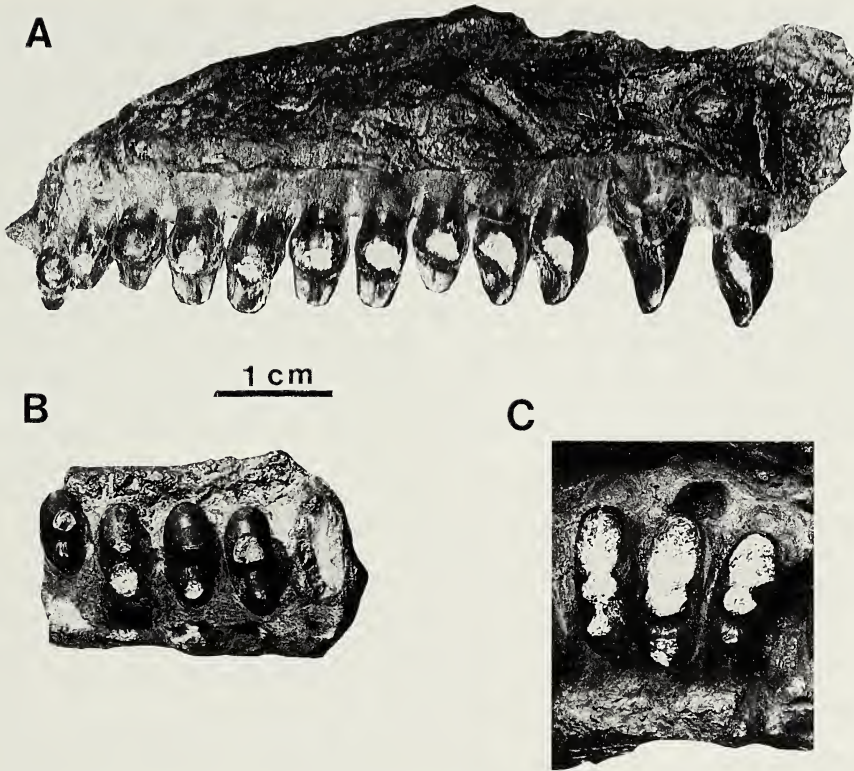


Fig. 6.—Maxillary dentitions of adult *Desmatodon* and *Diadectes* specimens to illustrate attrition patterns of cheek teeth. A, medial view of left maxilla of *Desmatodon hesperis* (CM 47654); B, occlusal view of portion of left maxilla (anterior to left) of *Desmatodon hollandi* (CM 1938) containing teeth 5–8 and the root of 9; and C, occlusal view of portion of right maxilla (anterior to left) of *Diadectes lentus* (UC 675) showing teeth 7–9. Wear facets have been whitened.

approximately the same size. The cheek teeth of MCZ 2989 also exhibit the same reversed pattern of attrition that does not include the crown tips (Lewis and Vaughn, 1965).

Some confirmation on the above hypothesis of occlusion of the cheek teeth of diadectids can be found in the dentition of the nearly complete juvenile right maxilla of *Desmatodon hesperis* CM 47668 (formally UCLA VP 1748) described by Vaughn (1972). By way of comparison, its estimated length of about 55 mm is perhaps only 5 mm greater than that of the maxilla in AMNH 4346. With regard to this discussion, most notable about the maxillary dentition in CM 47668, consisting of eight complete teeth representing the entire series, is the absence of any signs of attrition. This might indicate that during mastication there was little or no direct occlusion between the upper and lower cheek teeth, but rather they occluded principally with the inner surface of the lower jaw parapet. As was pointed out by Vaughn (1972), rapid tooth replacement offers an alternative but less satisfactory explanation for the absence of wear facets in CM 47668.

In the development to full maturity the cheek teeth of *Diadectes* undergo a number of profound morphological changes that result in a much greater degree of molarization (Fig. 6C): 1) dramatic increase in transverse expansion; 2) strong

reduction in the prominence of the central cusp, which in the maxillary and dentary dentitions occupy positions labial and lingual to the center of the crowns, respectively; and 3) development of prominent, shoulder-like cusps on the labial and lingual margins of the crown which subsequently acquire true cusps. The attrition pattern of the cheek teeth in adult specimens of *Diadectes* is also more complicated than in juveniles and progresses typically through four stages before tooth replacement occurs (Fig. 6C): **stage 1**, in the maxillary cheek teeth a sub-circular wear facet occurs on the lingual shoulder cusp and on the lingual side of the central cusp, whereas in the dentary cheek teeth the reverse pattern occurs, with the wear facets appearing on the labial shoulder cusp and the labial side of the central cusp; **stage 2**, the wear facets of the shoulder and central cusps of stage 1 enlarge and merge to produce a single principal wear facet that is flat or slightly concave, and an additional small subcircular facet appears on the shoulder cusp on the opposite side of the crown as the principal wear facet; **stage 3**, the principal and shoulder-cusp wear facets of stage 2 enlarge and partially merge, with an eventual loss of the central and shoulder cusps of the principal facet; and **stage 4**, extreme attrition produces a single flat or slightly concave wear facet that may extend nearly the entire transverse width of the crown.

In mature specimens of *Desmatodon* the cheek teeth never acquire the advance molarization features seen in mature specimens of *Diadectes* (Vaughn, 1969, 1972; Berman and Sumida, 1995). In this regard, the most notable differences of the cheek teeth of *Desmatodon hesperis* include (Fig. 6A): 1) transverse expansion is only moderate; 2) central cusp remains very prominent; 3) lingual and labial shoulders of the crown are only moderately developed and do not possess true cusps; and 4) lingual, shoulder-like cusp is more sharply defined than the labial shoulder-like cusp in the cheek teeth of the maxillary, because the base of the central cusp is much more expanded laterally than it is medially, whereas the reverse condition is true in the cheek teeth of the dentary. Along with a lesser degree of molarization, the degree of attrition of the cheek teeth in adult specimens of *D. hesperis* is limited to a subcircular facet on the lingual and labial shoulder-like cusps in those of the maxilla and dentary, respectively (Fig. 6A). It is also interesting that in adult specimens of *D. hesperis* almost all of the maxillary cheek teeth exhibit attrition, whereas only rarely do those of the dentary. As examples, in the complete dentition of the holotypic left maxilla CM 47654 (Fig. 6A; formally UCLA VP 1706) and in the five cheek teeth of the partial right maxilla CM 47677 of *D. hesperis* a distinct wear facet occurs on all the teeth except for two far posterior cheek teeth in CM 47654 (Vaughn, 1969, 1972). This is contrasted by the complete dentitions of the right lower jaw CM 47670 and left dentary CM 47676 of *D. hesperis* in which the number of cheek teeth exhibiting wear facets is only three and one, respectively (Berman and Sumida, 1995:fig. 3, 4). The above features of attrition suggest that occlusion between the upper and lower cheek teeth was not only restricted to a lingual-labial or side-to-side contact, but, as suggested by the dentary dentitions, in some instances was greatly reduced and, therefore, similar to the condition in very juvenile specimens of *Diadectes*. In the four cheek teeth of the presumed adult holotypic left maxilla CM 1938 (Fig. 6B) and only-described specimen of *D. hollandi* the degree of molarization and attrition is basically intermediate between those of *D. hesperis* and adults of *Diadectes*. Greater transverse expansion of the cheek teeth in CM 1938 is accompanied by reduction in the prominence of the central cusp and the development of well-defined labial and lingual shoulders that lack true cusps, and

attrition can be described as characterizing stage 1 in adult specimens of *Diadectes*. It is concluded from these features that in CM 1938 occlusion between upper and lower cheek teeth had begun to shift to a principally dorsoventral, vertical alignment between the upper crown surfaces. This agrees with the observation (Vaughn, 1969, 1972; Berman and Sumida, 1995) that the cheek-tooth dentition in *D. hollandi* is more advanced than that in *D. hesperis*.

The preceding discussion suggests that with the increased transverse expansion of the cheek teeth in *Diadectes* and *Desmatodon*, either as a result of ontogenetic development or evolution, the occlusion between the crowns of the upper and lower series shifts from an exclusively side-to-side contact to one in which there is an increasingly more vertical alignment and a strictly dorsoventral contact between the upper surfaces of the crowns. It is assumed, although not possible to demonstrate, that mastication in adults of *Diadectes* and *Desmatodon* still involved contact between the upper cheek teeth and the parapet of the lower jaw and the lower cheek teeth and the ventral surface of the secondary palatal shelf of the palatine.

Considering the large number of *Diadectes* specimens available for study, it seems more than coincidental that the sort of double-toothed row preservation of the cheek teeth seen in the juveniles AMNH 4346 and MCZ 9331 has not been reported in any of the far more plentiful adult specimens. The obvious explanation would seem to be that only in extremely juvenile specimens do the upper and lower cheek-tooth series occupy a strictly side-to-side relationship to one another, whether or not they are actively engaged in mastication. If, therefore, postmortem breakage occurs along the jaw line in an extremely juvenile specimen in which the lower jaws are tightly joined to the skull, it is not likely to result in a complete separation between the upper and lower cheek-tooth series, but rather would produce the double-toothed row condition seen in AMNH 4346 and MCZ 9331. On the other hand, under the same circumstances adult specimens of *Diadectes* would not be expected to produce the same double-toothed row condition, as their opposing cheek-tooth series occlude exclusively between the upper crown surfaces. Although only rarely is it possible to examine the cheek teeth in a resting state of occlusion in a mature, undistorted specimen of *Diadectes*, one unusual example is available. The *Diadectes* skull CM 24127 from the Early Permian Washington Formation of West Virginia is uniquely preserved as an internal mold of an undistorted skull and mandible that faithfully reproduces anatomical features (Berman, 1971). Most importantly, the lower jaws are in their proper orientation, so that the resting, occlusal state of the upper and lower cheek teeth can be clearly interpreted. Although the lateral margin of the dentition is not represented, latex casts allowed a detailed description of all other aspects of the cheek-tooth series (Berman, 1971). Not only do they exhibit an advanced stage of molarization and a reversed pattern of attrition, with many teeth attaining at least an advanced stage 3 of wear, but also a large degree of dorsoventral occlusion between the upper surfaces of the opposing crowns.

Hotton et al. (1997) presented a compelling argument that *Diadectes*, as well as *Desmatodon*, was primarily adapted to a diet of high-fiber terrestrial vegetation. Their evidence relied almost exclusively on the complex dental adaptations that allowed for the collection and mechanical processing of a wide variety of plant tissues. It was also argued that the large size and body proportions of diadectids, particularly their bulky, rotund torsos, are suggestive of the possession of a disproportionately large gut needed for the endomicrobial fermentation of plant cel-

lulose. The conclusions of Hotton et al., however, were obviously based on observations of adult specimens, and, as noted above, juveniles of *Diadectes* exhibit striking differences in their cheek dentitions and the manner in which they occluded. In particular, the cheek teeth of juveniles are far less molariform and the area of occlusion is not only much more limited in area, but is restricted to the lingual and labial, rather than the dorsal, margins of the crowns, and thus must have been far less effective in the comminution of plant tissues. These comparisons raise the question of whether the dentition of juvenile *Diadectes* was capable of processing terrestrial vegetation as efficiently and of equivalent toughness or fiber content as that consumed by adults. Changes in the dentition from juveniles to adults are too great not to suspect that they were not accompanied by a change in diet; perhaps the juveniles were primarily insectivorous or were omnivorous but restricted to low-fiber vegetation. Thus, our interpretation of the ontogeny of diadectid dentition and mastication lends strong support to preliminary observations by Vaughn (1972:25) that changes in the maxillary dentition in *Desmatodon hesperis* from juvenile to adult may have paralleled a shift in dietary habit.

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ARCHAEOLOGY OF TRANTS, MONTSERRAT. PART 4.
FLAKED STONE AND STONE BEAD INDUSTRIESJOHN G. CROCK¹ROBERT N. BARTONE²

ABSTRACT

Trants is one of the earliest Ceramic period sites known anywhere in the Caribbean. Attribute analysis of lithic materials from the Trants site (MS-G1) has determined the reduction processes associated with early Ceramic, or "Saladoid," period flaked stone and stone bead industries. Both industries feature the systematic, on-site reduction of exotic lithic materials. The flaked stone industry is characterized by the expedient production of flakes for utilitarian purposes, with little investment in tools having fixed morphologies. In contrast, the production of stone bead ornaments is characterized by a more complicated and labor-intensive process. This article describes the reduction sequences and compares the general attributes of the Trants assemblages to lithic industries known elsewhere in the region.

KEY WORDS: Trants site, lithic analysis, flaked stone, stone bead, grater board teeth hypothesis

INTRODUCTION

The Trants site (MS-G1) is located on the windward coast of Montserrat, a small volcanic island in the northern Lesser Antilles (Fig. 1). This article focuses on lithic industries represented at the Trants site, specifically flake production and stone bead manufacture, both of which exhibit flaked-stone reduction techniques. This is the fourth in a series of articles concerned with Trants; other articles deal with field methods (Watters, 1994), vertebrate fauna (Reitz, 1994), and settlement data (Petersen, 1996), respectively. All of the lithic materials discussed here were recovered during archaeological investigations conducted at Trants in 1979 (Watters, 1980) and 1990 (Petersen and Watters, 1993). Specimens studied were recovered during controlled excavation of 1.0 m × 1.0 m or 2.0 m × 2.0 test units, or during systematic surface collections.

Following the 1990 fieldwork, flaked-stone artifacts were analyzed to characterize the Saladoid period lithic industries represented at the site. The Saladoid occupation at Trants can be dated ca. 500 B.C.–A.D. 300, and likely later. Two flaked-stone industries were identified during the study, both employing nonlocal materials. The first industry involved the production of flakes and fragments for use. The second industry involved the manufacture of stone bead ornaments.

The preliminary results of this analysis were presented at the 14th International Congress for Caribbean Archaeology (Bartone and Crock, 1993). These results are developed further here through a comparison with similar investigations and relevant observations from other Caribbean sites. This article also uses these data to evaluate the hypothesis that reduction of chert was primarily geared toward the production of microliths for use as teeth in wooden grater boards.

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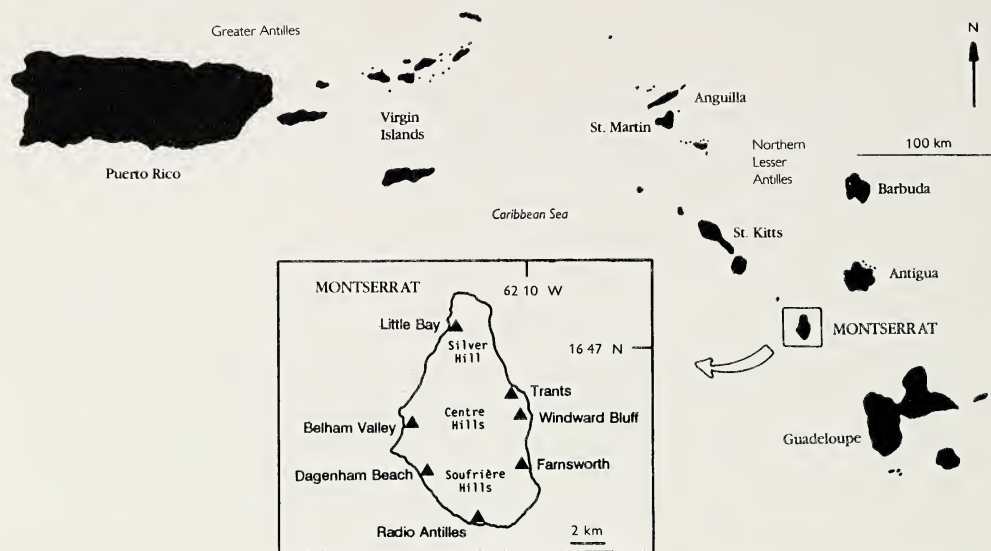


Fig. 1.—Map of the northern Lesser Antilles showing the location of the prehistoric Trants site, located on the east coast of Montserrat.

MATERIALS AND METHODS

A total of 2436 lithic artifacts recovered from the Trants site in 1979 and 1990 were analyzed (Bartone and Crock, 1993). Of this total, approximately one-half ($n = 1238$) was recovered during systematic surface collections and one-half ($n = 1198$) during controlled, 1.0 m \times 1.0 m (1990) and 2.0 m \times 2.0 m (1979) test unit excavations (Table 1). Excavated materials were recovered from both 6.4 mm mesh (41%) and finer 3.2 mm mesh (59%) screens. A portion of the total 1990 lithic inventory remains unanalyzed, including specimens recovered from 0.5 m \times 0.5 m test pits, some additional 3.2 mm mesh samples, and all material recovered from 1 mm mesh screening of feature sediment.

The general format of the analysis followed a processual model developed by Collins (1975) with consideration given to the analytical techniques employed by Crabtree (1982). The approach focused on technological aspects of reduction processes and expressly avoided the use of functional categories during analysis. As noted by Pantel (1988:18), the identification of gross tool types based on function has inherent limitations for the Caribbean because most existing typologies and tool classification systems have been developed for North American and European lithic assemblages.

Lithic analysis began with the separation of materials related to stone flake production from those associated with stone bead manufacture. This distinction was based on artifact shape and raw material. Once separated, all artifacts were placed into process-oriented categories based on the stage of reduction they represented. Following assignment to categories, the dimensions and weights of all artifacts were recorded (Table 2), along with attributes specific to each artifact class.

For flake production material (predominantly chert), the primary categories include unmodified raw material, core, core fragment, flake, fragmentary flake,

Table 1.—*Vertical distribution of flaked stone artifacts recovered during test unit excavation at the Trants site (MS-G1), Montserrat.*

Unit/level/ stratum	¹⁴ C dates	Cores/ core frags.	Core tools	Flake debitage	Util./ Mod. Debitage	Bead preforms	Fully shaped beads	Bead debitage	Total
N396 E571 (1.0 × 1.0 m)									
0–10 A				16	2				18
10–20 A				25	1				26
20–30 B				9	1				10
30–40 B				5	2		1		8
40–50 B		1		23					24
50–60 C	480 BC ± 80			28	2	1	1	3	35
60–70 C	480 BC ± 80			1		1			2
70–80 C				4					4
80–90 C				1					1
Unit Total		1	0	112	8	2	2	3	128
N421 E645 (1.0 × 1.0 m)									
0–10 A				31					31
10–20 A				86		1	1	1	89
20–30 A				18	1				19
20–30 B				39					39
30–40 B				19		1		2	22
40–50 B				8					8
50–60 B				2					2
60–70 B				1					1
60–70 C	AD 210 ± 90	1		60	1			5	67
70–80 C	10 BC ± 90			143			1		144
80–90 C				21					21
80–90 D				3					3
90–100 C				1					1
90–100 D				4					4
Unit Total		1	0	436	2	2	2	8	451
N596 E571 (1.0 × 1.0 m)									
0–10 A		1		21	1	1	1		25
10–20 A				25	1			1	27
20–30 A				33	3				36
30–40 B	AD 60 ± 70	1		54			5	1	61
40–50 B				27	2	1			30
50–60 B				14			1	1	16
60–70 B				17			3		20
70–80 B	440 BC ± 90			4			1		5
80–90 C				2					2
Unit Total		2	0	197	7	2	11	3	222
1979 T. U. (2.0 × 2.0 m)									
0–10		4		63	2			1	70
10–20		1	1	102	9	1		5	119
20–30		2		74	7			4	87
30–40				43	7	1		2	53
40–50		3	1	39	1				44
50–60		1		18	4				23
60–70				1					1
Unit Total		11	2	340	30	2	0	12	397
Total Lithics		15	2	1085	47	8	15	26	1198

Table 2.—Mean and range of the weight, length, width, thickness, and maximum dimension for lithic artifact categories represented at the Trans site (MS-G1), Montserrat.

Category	Count	Weight (g)	Length (cm)	Width (cm)	Thick. (cm)	Max. dim. (cm)
Flake Production Material						
Core	75	Mean 40.12 Range 2.86–345.20	Mean 4.29 Range 2.28–9.85	Mean 3.26 Range 1.86–8.05	Mean 2.16 Range 1.00–5.71	Mean 4.29 Range 2.28–9.85
Core Fragment	5	Mean 13.34 Range 3.03–28.75	Mean 3.20 Range 1.88–4.21	Mean 2.29 Range 1.37–3.63	Mean 1.42 Range 0.83–2.42	Mean 3.20 Range 1.88–4.21
Core Tool	12	Mean 36.86 Range 5.42–130.00	Mean 4.34 Range 2.53–7.07	Mean 3.28 Range 2.42–4.62	Mean 2.26 Range 1.00–4.34	Mean 4.34 Range 2.53–7.07
Complete Flakes	1120	Mean **2.26 Range <0.01–43.85	Mean 1.70 Range 0.08–6.33	Mean 1.60 Range 0.21–7.89	Mean 0.52 Range 0.01–3.84	Mean 1.93 Range 0.38–7.89
Utilized	131	Mean 7.32 Range 0.17–71.85	Mean 2.81 Range 0.97–6.55	Mean 2.53 Range 0.74–7.54	Mean 0.93 Range 0.23–2.43	Mean 3.14 Range 1.00–7.54
Complete Flakes	3	Mean 17.06 Range 5.60–39.24	Mean 2.85 Range 2.19–4.05	Mean 3.76 Range 3.07–4.90	Mean 1.19 Range 0.64–2.07	Mean 3.76 Range 3.07–4.90
Modified Flakes	409	Mean *1.53 Range <0.01–33.21	Mean 1.52 Range 0.09–5.29	Mean 1.35 Range 0.19–6.29	Mean 0.44 Range 0.02–1.92	Mean 1.706 Range 0.35–6.29
Fragmentary Flakes	46	Mean 4.45 Range 0.30–18.33	Mean 2.40 Range 0.66–4.84	Mean 2.11 Range 0.83–4.26	Mean 0.76 Range 0.15–1.89	Mean 2.66 Range 1.29–4.84
Utilized	505	Mean ***3.18 Range <0.01–213.80	Mean 1.75 Range 0.07–9.76	Mean 1.23 Range 0.12–7.24	Mean 0.74 Range 0.05–5.37	Mean 1.77 Range 0.36–9.76
Fragmentary Flakes	38	Mean 5.96 Range 0.21–16.63	Mean 3.00 Range 0.90–4.72	Mean 1.85 Range 0.81–3.36	Mean 1.12 Range 0.07–2.00	Mean 3.02 Range 0.90–4.72
Utilized	3	Mean 6.69 Range 3.79–9.26	Mean 2.64 Range 2.02–3.02	Mean 2.11 Range 1.79–2.35	Mean 1.46 Range 1.13–1.86	Mean 2.64 Range 2.02–3.02
Bead Production Material						
Bead Debitage	25	Mean ****2.10 Range <0.01–20.89	Mean 1.44 Range 0.46–3.60	Mean 1.28 Range 0.33–4.55	Mean 0.48 Range 0.09–1.88	Mean 1.54 Range 0.46–4.55
Flakes	21	Mean ***0.84 Range <0.01–2.83	Mean 1.25 Range 0.32–2.31	Mean 0.87 Range 0.07–1.52	Mean 0.61 Range 0.03–1.40	Mean 1.26 Range 0.40–2.31
Bead Debitage	12	Mean 7.28 Range 0.92–38.18	Mean 2.29 Range 1.07–4.48	Mean 1.79 Range 0.77–3.58	Mean 1.09 Range 0.55–2.09	Mean 2.3 Range 1.07–4.48
Fragments	19	Mean 4.97 Range 0.45–14.94	Mean 2.11 Range 1.00–3.55	Mean 1.49 Range 0.85–2.13	Mean 1.21 Range 0.33–2.07	Mean 2.11 Range 1.00–3.55
Bead Preform 1	12	Mean 3.28 Range 0.90–7.30	Mean 2.20 Range 1.70–3.67	Mean 1.45 Range 0.91–2.08	Mean 0.92 Range 0.45–1.38	Mean 2.20 Range 1.70–3.67
Bead Preform 2	12					
Bead Preform 3	12					
Total	2436					

* Weight does not include 37 specimens which weigh less than 0.01 g each.
 ** Weight does not include 17 specimens which weigh less than 0.01 g each.
 *** Weight does not include seven specimens which weigh less than 0.01 g each.
 **** Weight does not include one specimen which weighs less than 0.01 g.

and undifferentiated fragment. For cores and core fragments, attributes include the number of flake scars present, the percentage of cobble cortex remaining, and the presence or absence of platform preparation. For flakes, attributes include portion (i.e., complete, longitudinal, distal, proximal), platform type (i.e., unifacial, crushed, faceted), distal features (i.e., feathered, hinged, or step-terminated), percentage of cortex remaining, and the presence or absence of platform preparation.

Concurrent with the attribute analysis, all flake production materials were analyzed for possible use wear and/or intentional modification. Since magnification is critical in discerning natural damage from human use, all analyses were conducted with the aid of a 10–30× Bausch and Lomb binocular microscope. Where use wear (defined as incidental edge damage or polish) and/or intentional modification (defined as pressure-flaked edge alteration or retouch) were identified, such artifacts were placed in various categories; these include utilized flake, utilized fragmentary flake, utilized fragment, modified flake, and modified fragment. Specific attributes of all such flake tools were recorded; for utilized and modified flakes and fragments, these attributes include details such as the size of scars caused by use or retouch, and the percentage of tool margin exhibiting unnatural alteration.

For bead materials, the categories include bead preforms, fully shaped beads, bead material flakes, and bead material fragments. Artifacts assigned to the bead preform category were subsequently divided into three graduated stages to further characterize the reduction process (Bead Preform 1–3). Fully shaped beads, including completely drilled and partially drilled specimens, were categorized as “fully shaped.”

FLAKE PRODUCTION

Raw Material and Reduction Technique

Several nearly complete nodules and a high percentage of cortex on many of the cores and core fragments (37%) indicate that whole, unmodified cobbles and pebbles were transported to the Trants site prior to being flaked (Bartone and Crock, 1993). All of the chert recovered from the island is presumably nonlocal as there are no known chert deposits on Montserrat. The dominant lithic raw material is a tan and brown chert (80% of the total sample), all of which probably originated in neighboring Antigua (Fig. 2). The most abundant and accessible source is Flinty Bay, Long Island, which lies approximately 1.6 km off the island of Antigua and 40 km northeast of Montserrat. Alternative chert sources in Antigua are under investigation (Watters and Donahue, 1990; Gijn, 1993; Knippenberg, 1995). The sources for other types of chert identified at Trants remain unknown (Fig. 3).

Eighty-five of the 92 cores and core fragments (92%) exhibit large, convex flake scars and little evidence of preparation. These attributes confirm that direct, freehand percussion was the most common method of reducing chert pebbles and cobbles once they arrived at Trants (see Fig. 2, 3). A smaller number of cores and core fragments ($n = 7$, or 8%) provide evidence of bipolar percussion, a reduction technique used instead of, or in addition to, striking flakes off a core freehand. Bipolar cores are characterized by crushed ends which exhibit linear, often step-terminated flake scars and diffuse evidence of bulbs of percussion; bipolar battering typically occurs on opposing margins (Fig. 4). Bipolar percussion



Fig. 2.—Antigua chert "freehand" cores recovered from the Trants site (MS-G1), Montserrat.

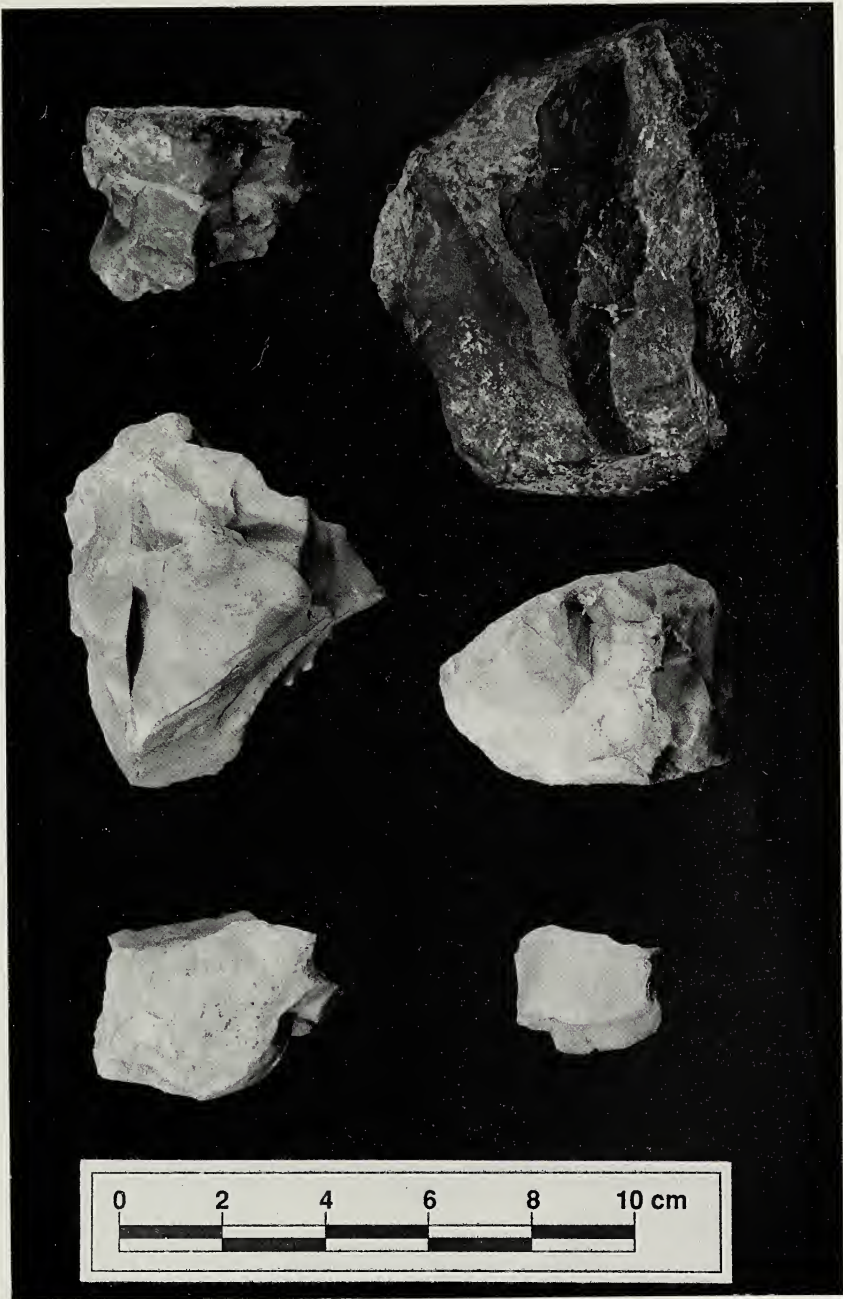


Fig. 3.—“Freehand” cores of exotic chert from unknown sources recovered from the Trants site (MS-G1), Montserrat.

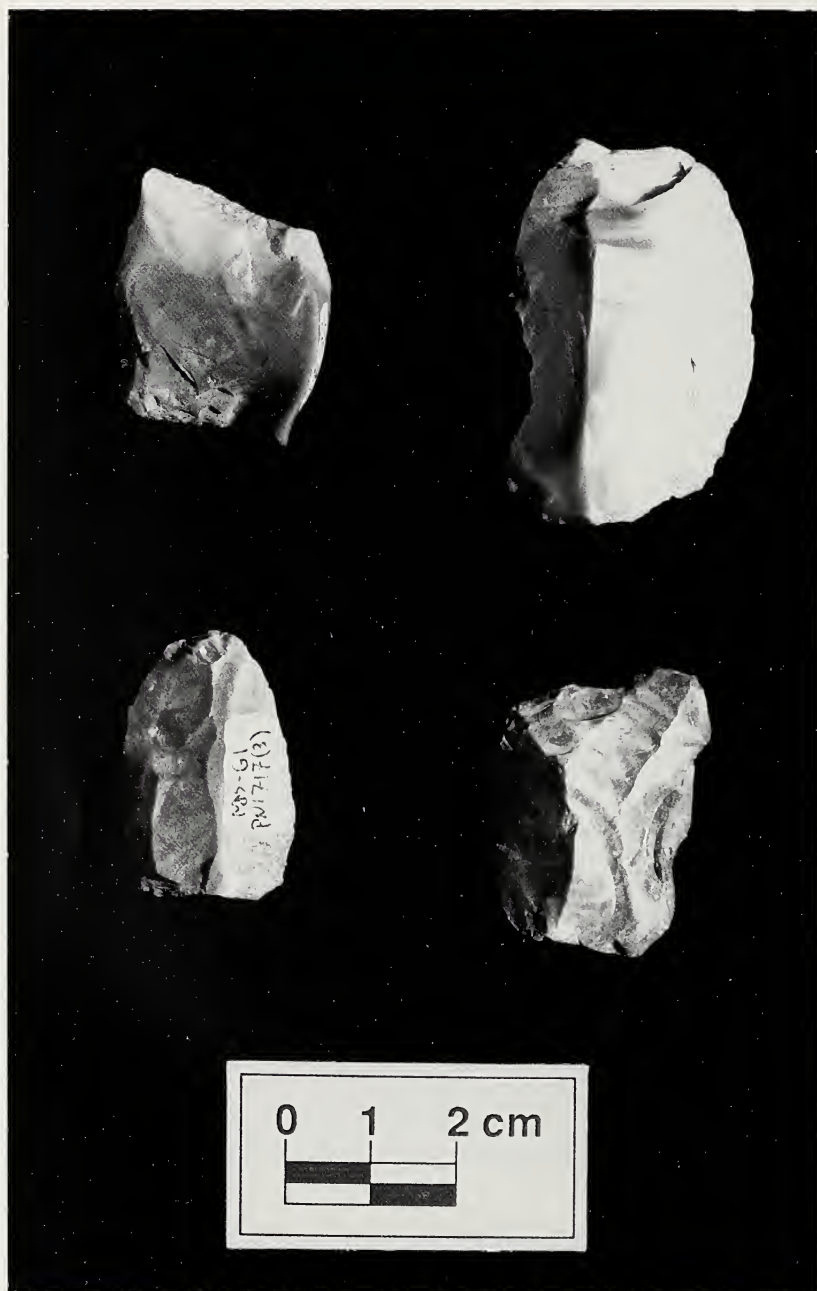


Fig. 4.—Bipolar cores recovered from the Trants site (MS-G1), Montserrat.

involves resting one end of the core on an anvil and striking flakes off the opposite end. This technique is well suited for reducing smaller, more tabular cores and fragments, and the expedient production of smaller, more angular flakes and fragments for immediate use (e.g., Shott, 1989).

In North America, some researchers argue that lithic artifacts with crushing and flake scars on opposing margins are not cores at all but instead are tools which were used to split bone and/or wood (e.g., LeBlanc, 1992). In Caribbean contexts, however, it makes more sense that bipolar battered artifacts are cores given the paucity of large mammals in the region prehistorically (e.g., Steadman et al., 1984; Wing, 1989; Pregill et al., 1994; Reitz, 1994), and the presence of both shell and ground stone woodworking tools.

Flake Production and Utilization

The predominance of freehand percussion and lack of formed tools indicate that the inhabitants of Trants were reducing raw material to produce simple flake tools and/or microliths, and investing no time in the production of uniform tool types. Relatively high percentages of utilized flakes and fragments in the lithic sample indicate that the production of flakes for use was indeed a major output of the flaked stone industry at Trants. Evidence of use wear identified in the Trants assemblage includes small microflake scars along utilized edge(s), and/or edge polish (Fig. 5, 6).

In the sample of complete flakes identified ($n = 1120$), 12% ($n = 131$) exhibit use wear; while of the fragmentary flakes ($n = 409$), 11% ($n = 46$) exhibit use wear; and of the fragments ($n = 505$), 7% ($n = 38$) exhibit use wear. Intentional modification, or the purposeful alteration of post-percussion morphology, is extremely rare in the sample, with only 0.2% ($n = 3$) of complete flakes and 0.2% ($n = 3$) of lithic fragments being intentionally modified.

Many utilized flakes and fragments ($n = 44$, or 21%) exhibit one or more types of edge wear on several margins. Such extensive usage suggests that they were recycled by one or more individuals over time, perhaps as readily available "pick-up" tools (Bartone and Crock, 1993). Of the extensively utilized flakes and fragments, 18 (41%) exhibit a specific type of damage characterized by at least one sharply incurvate edge (Fig. 7). The similarity of edge damage among these tools suggests that they were used to perform similar tasks.

Although lithic reduction was expedient and done to produce flakes rather than formed tools, the selection of flakes for use was far from random with respect to size. The mean maximum dimension of pieces selected for use is considerably larger than the mean maximum dimension of those that were not (Fig. 8). In the case of complete flakes, for example, a standard t -test reveals that the difference in mean maximum dimension between complete flakes and utilized complete flakes is significant ($t = -12.275$, $p = <0.001$).

Beyond a clear bias in favor of significantly larger pieces, there appears to be an absence of a specific "target" size, however. The size of utilized flakes and fragments ranges widely (see Table 2). Comparable emphasis on larger lithic specimens within a given sample is well known elsewhere (e.g., Keeley, 1993: fig. 5.1).

The major portion of the flake production inventory (ca. 90%) is unutilized debitage, or specimens which do not demonstrate use wear. Some characteristics of this large portion of the lithic inventory suggest that there may be an as yet

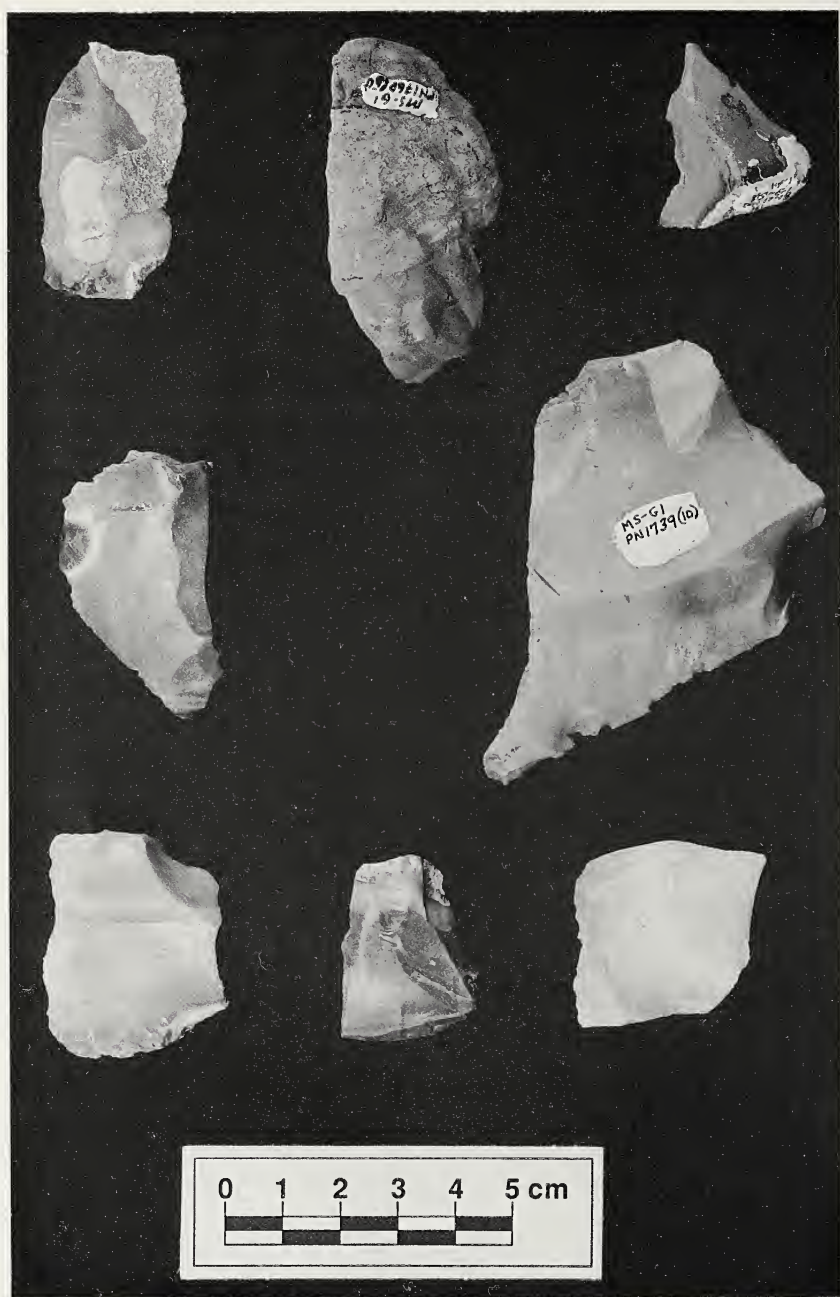


Fig. 5.—Utilized flakes recovered from the Trants site (MS-G1), Montserrat. Note utilized edges face left.

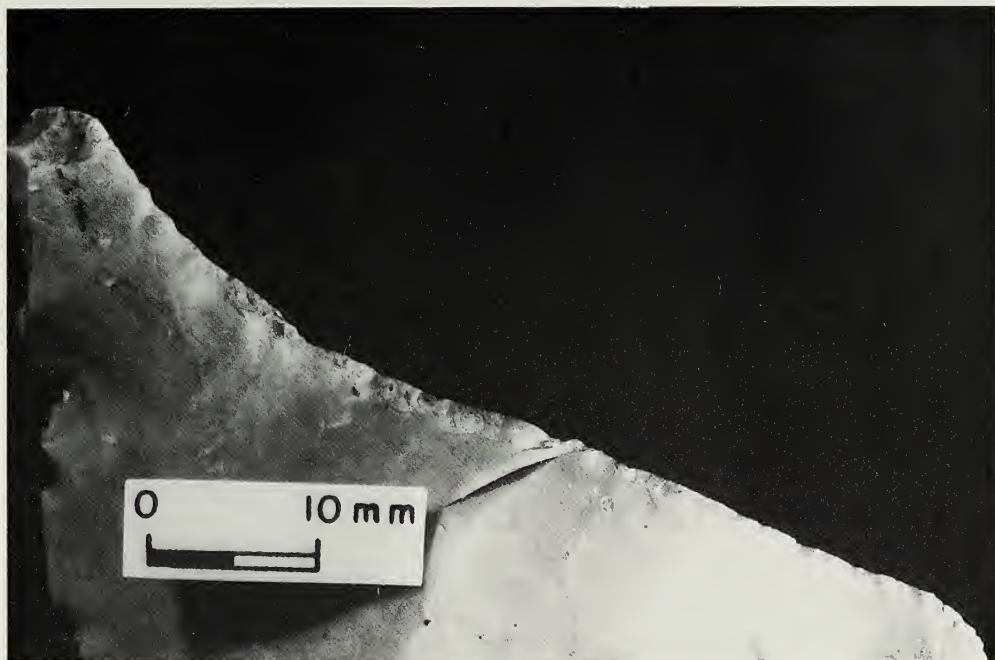


Fig. 6.—Close up of edge damage exhibited by a utilized flake recovered from the Trants site (MS-G1), Montserrat.

unidentified goal of lithic reduction at Trants. Frequency distributions indicate that a high percentage (76%) of unutilized specimens have a maximum dimension between 5 mm and 25 mm (Fig. 9). This size consistency may indicate that flakes were being produced for purposes other than for use as simple, singular tools. One possibility is that microliths were being produced for insertion as “teeth” into composite tools used for tasks such as cutting or grating.

Saladoid Period Flaked Stone Industries

Analyses of flake production artifacts from other Saladoid sites indicate that, like Trants, raw materials were transported from the source to the site prior to being reduced. The presence of large cores and primary reduction flakes documents this pattern at sites such as Hacienda Grande in Puerto Rico (Walker, 1985), Hope Estate in St. Martin (Haviser, 1988), Sugar Factory Pier in St. Kitts (Walker, 1980), and Pearls in Grenada (Cody, 1990). All of these sites are attributable to the Saladoid period, which was the earliest widespread ceramic-using manifestation in the West Indies, generally dated ca. 500 B.C.—A.D. 600. Artifact inventories from these sites, like Trants, include various exotic lithic raw materials, and they provide evidence of extensive trade networks during this period.

Assemblages from other Saladoid period sites also provide evidence of both freehand and bipolar reduction of lithic raw materials. While freehand percussion seems to have been the preferred method of reduction at Trants, bipolar reduction apparently was the dominant technique employed at other Saladoid period sites, including Hacienda Grande in Puerto Rico and Sugar Factory Pier in St. Kitts (Walker, 1985). Walker (1980) suggests that bipolar cores are evidence of the



Fig. 7.—Extensively utilized flakes exhibiting at least one incurvate edge recovered from the Trants site (MS-G1), Montserrat.

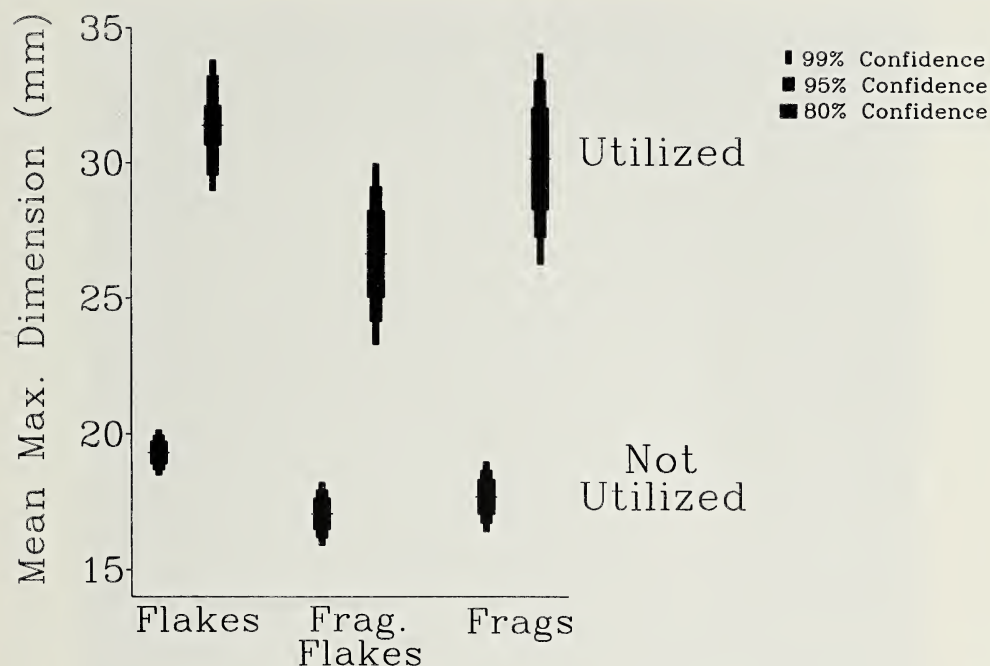


Fig. 8.—Mean maximum dimension and error ranges associated with utilized and nonutilized complete flakes, fragmentary flakes, and undifferentiated fragments recovered from the Trants site (MS-G1), Montserrat.

production of small, angular fragments used as “teeth” in manioc grater boards. Small flakes also have been attributed to manioc processing at several other Saladoid sites, including Pearls in Grenada (Cody, 1990) and, with some reservation, Seguneau in Martinique (Allaire, 1985).

The Grater Teeth Hypothesis

Production of flakes for insertion into wood as grater board teeth has been reported ethnographically among the Wai Wai and other related groups in mainland South America (e.g., Roth, 1924; Evans and Meggers, 1960:250; Yde, 1965) (Fig. 10). Existence of flake-toothed grater boards also has been documented archaeologically for the late prehistoric or historic Taino of Cuba, where one was discovered in a cave site (Harrington, 1921:98).

Despite archaeological and ethnographic support for stone grater teeth production among Amerindians in the Caribbean and lowland South America, their presence cannot be proven solely on the basis of bipolar cores and small angular flakes. Among other issues, DeBoer (1975) reported ethnographic evidence of a wide range of other materials used for the teeth in manioc graters, including wood splints, palm thorns, bone, animal teeth, and shell. DeBoer also warned that at sites where ceramic griddles and griddle fragments have been taken as evidence of manioc preparation, they may have been alternatively used to grill maize tortillas and not manioc. Therefore, he questioned the blanket assertion that flaked stone assemblages are attributable to the production of stone grater teeth for manioc processing.

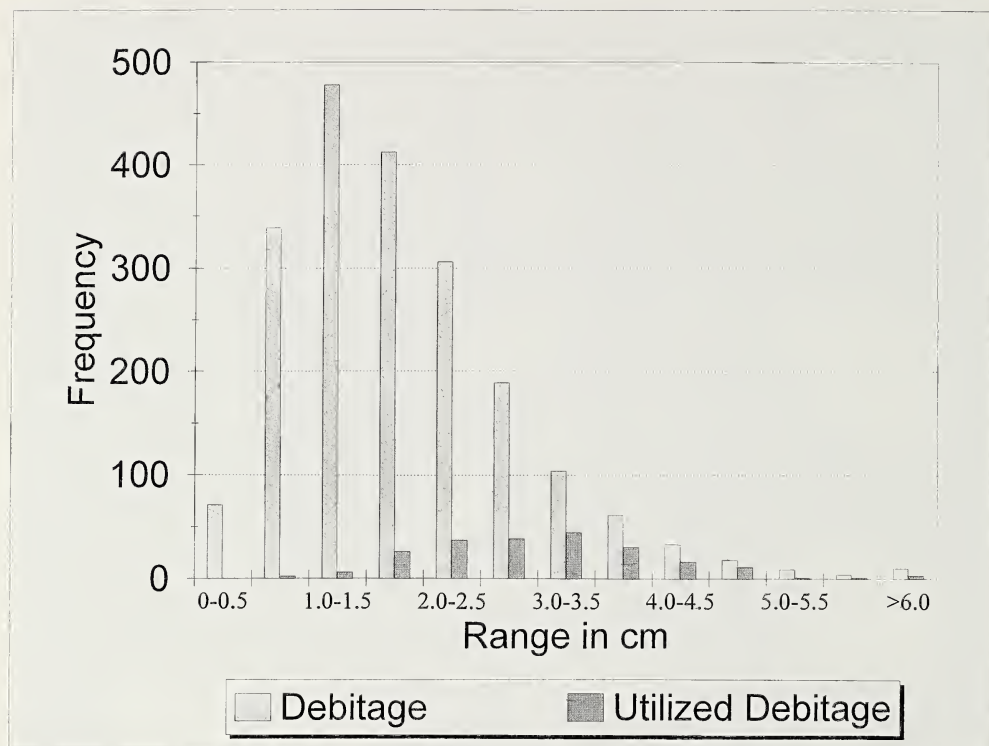


Fig. 9.—Histogram showing frequencies by maximum dimension of utilized and nonutilizeddebitage from the Trants site (MS-G1), Montserrat.

Walker (1983) addressed some of these concerns by conducting use-wear analysis of flakes from the Sugar Factory Pier site in St. Kitts. Using replicated grater board flakes, the size of which was based on ethnographic samples (after DeBoer, 1975), Walker developed a control for measuring length of use, potential function, and degree of polish. He then compared the replicated sample to flakes recovered archaeologically and made a strong case for the presence of grater teeth manufacture at the Sugar Factory Pier site. The maximum dimension of grater board teeth in Walker's replicated and archaeological samples ranged from 2 mm to 10 mm (Walker, 1980:111).

If the main output of flake production at Trants was indeed grater board teeth, then, based on Walker's study, there should be a clustering of utilized and unutilized flakes roughly within the range of 2 mm to 10 mm. The Trants data show no such groupings. Instead, the Trants data show clear preference for the use of flakes with maximum dimensions greater than 15 mm and no clear size clusters whatsoever. Only a handful of the utilized flakes identified in the lithic sample from Trants even fit the size criteria as defined by Walker.

The Trants data do not support the grater teeth hypothesis based on this line of evidence. The use of grater boards at Trants still cannot be ruled out, however. It may be that the use wear associated with this mode of abrasion is too subtle to be identified given the techniques and equipment employed in this study. It also is possible that the sample analyzed did not include flaked stone material

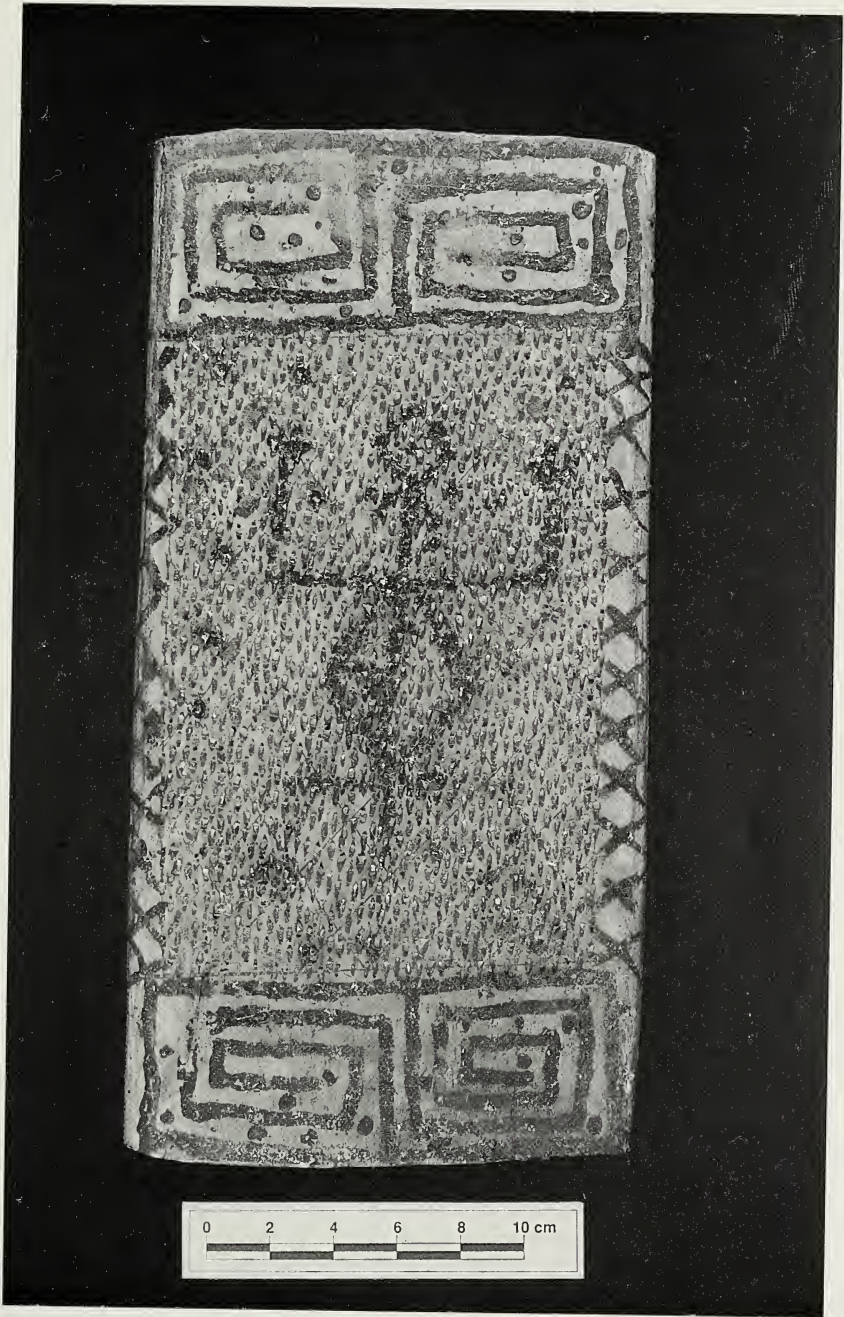


Fig. 10.—Wai Wai manioc grater board (specimen in the collection of James B. Petersen).

from specific areas of the site where grater board manufacture and/or use took place. Alternatively, grater boards may have been manufactured at only select sites (other than Trants) and traded widely, as is recorded for the Wai Wai and other groups in South America (Evans and Meggers, 1960:334, quoting Thurn, 1883; Yde, 1965:34; Chernela, 1992). As described by Mowat (1989:25): "Graters of the Arawakan and Tukanoan tribes were particularly prized as trade objects and would be exchanged for such items as blowpipes, pottery, hammocks and hunting dogs."

Whether or not the inhabitants of Trants and other Saladoid period sites actually produced grater boards, they clearly produced flakes for use as simple, expedient tools. The assumption that chert debitage is directly related to the production of grater boards has obscured the importance of flake tools in Saladoid period lithic assemblages in general. The results of the Trants study indicate that flake tools represent a significant output of the flake production industry and, as such, likely served a critical role in Saladoid lifeways at the site.

Beyond testing the grater teeth hypothesis, no attempt was made to attribute flake tools to specific functional categories, although likely uses include a host of everyday tasks such as scraping, cutting, smoothing, and engraving. The use of flake tools for such purposes is documented ethnohistorically among the Taino of the Greater Antilles and ethnographically among similarly adapted groups in lowland South America (e.g., Roth, 1924; Lovén, 1935; Rouse, 1948a). Ultimately, it may be possible to determine useful functional categories for flake tools in the Caribbean, but this will require more sophisticated analyses. It can be assumed, however, that artifacts with identical patterns of damage, for example, tools with sharply incurvate utilized edges, were used to perform the same or similar functions. Flake tool function also can be inferred from other archaeological evidence such as incised shell specimens.

BEAD PRODUCTION

Raw Material and Reduction Technique

Based on the analysis of 113 bead-related specimens from the 1979 and 1990 investigations, the Trants inhabitants were manufacturing stone beads at the site from raw materials such as white quartz, carnelian, feldspar, and jadeite or nephrite. None of these materials occur naturally in Montserrat and several, including nephrite, likely originated in mainland South America. Unaltered bead raw material arrived at Trants in the form of relatively small crystals and stone fragments, and these pieces were subsequently reduced and ultimately manufactured into beads.

Carnelian, a red-orange, translucent variety of microcrystalline chalcedony, is the most common material represented in the sample of bead-related specimens. Carnelian comprises the large majority of bead preforms (88%) and the majority of bead material debitage (65%). The source of this material remains unknown, although it likely originated outside of the Lesser Antilles, perhaps in South America or in the larger islands of the Greater Antilles (Cody, 1990).

Initial stages of bead manufacture employed flaked stone reduction techniques, hence bead manufacture is, in part, a flaked stone industry. First- and second-stage bead preforms exhibit small scars expanding inward from transverse margins indicating that excess material was flaked off in these stages. Some flaking in the first steps was probably done freehand, but given the small size of the flakes and

the need for greater control, pressure-flaking techniques likely were employed as well.

A total of 12 minimally altered artifacts were assigned to the category of Bead Preform 1 (Fig. 11), and 19 exhibiting further modification were assigned to Bead Preform 2. At the Bead Preform 2 stage, specimens were shaped into "block"-sized pieces suitable for further reduction (Fig. 12).

Artifacts grouped in the subsequent stage of bead manufacture ($n = 12$), designated Bead Preform 3, also exhibit small flake scars, but also have tiny pecked "pits" and abrasion striations, all of which indicate that pecking and/or grinding further transformed individual specimens at this stage of reduction (Fig. 13). In general, reduction at this level includes rounding and end tapering through the removal of the "sharp" edges and corners associated with the earlier preform "blocks."

In the final stage of bead manufacture, the bead raw material was fully shaped (designated Fully Shaped Bead). Specimens at this stage ($n = 23$) are characterized by the obliteration of all evidence of flaking and pecking through grinding and polishing (Fig. 14). Although exact techniques of grinding are uncertain, a grooved abrading stone curated at the National Trust Museum on Montserrat suggests one possible method. The flat stone has a narrow, rounded "track" engraved in its surface which may have been used to abrade beads during the manufacturing process.

The "fully shaped" category includes whole and fragmentary beads which have been partially or completely drilled. The majority of these beads exhibit biconical drill holes, indicating they were drilled from two directions with a pointed instrument (D. Watters, personal communication, 1992; Bartone and Crock, 1993). Several specimens reveal a remnant "cone" in unfinished drill holes, however, suggesting a hollow instrument may have been employed in some cases.

A greater variety of raw materials is represented in the "fully shaped" category, including material such as amethyst, which was not present in earlier stages of manufacture. These beads probably were manufactured elsewhere given that these materials occur only in finished bead form and not as preforms or debitage (Harrington, 1924; Bartone and Crock, 1993). Although the present study focuses on the reduction process and not on the definition of a finished bead typology, four general bead types were recognized among those grouped in the fully shaped category. These include small, flat "discoid" beads of various thicknesses, convex "barrel-shaped" beads of various lengths, cylindrical beads of various lengths, and beads produced through the minimal alteration of natural crystals (e.g., feldspar). Within these broad categories, beads vary in transverse section from fully rounded to multifaceted, depending on the material.

These types are roughly equivalent to those defined by Watters and Scaglione (1994) in a complementary study of 490 specimens in a private collection from the site. The beads and ornaments were collected from Trants in the early 20th century by planter S. W. Howes, whose original collection is currently curated by the National Museum of the American Indian, Smithsonian Institution (formerly the Museum of the American Indian, Heye Foundation). Based on the attribute analysis conducted by Watters and Scaglione (1994), the S. W. Howes collection contains finished beads manufactured from an even greater variety of materials (e.g., turquoise) and ornament types (e.g., zoomorphic pendants) which are unlike anything recovered during the 1979 and 1990 fieldwork. Watters and Scaglione (1994) grouped specimens by raw material and into preform ("blank") or finished



Fig. 11.—Unmodified and slightly altered bead raw materials (Bead Preform 1) recovered from the Trants site (MS-G1), Montserrat.



Fig. 12.—Minimally shaped bead materials (Bead Preform 2) recovered from the Trants site (MS-G1), Montserrat.

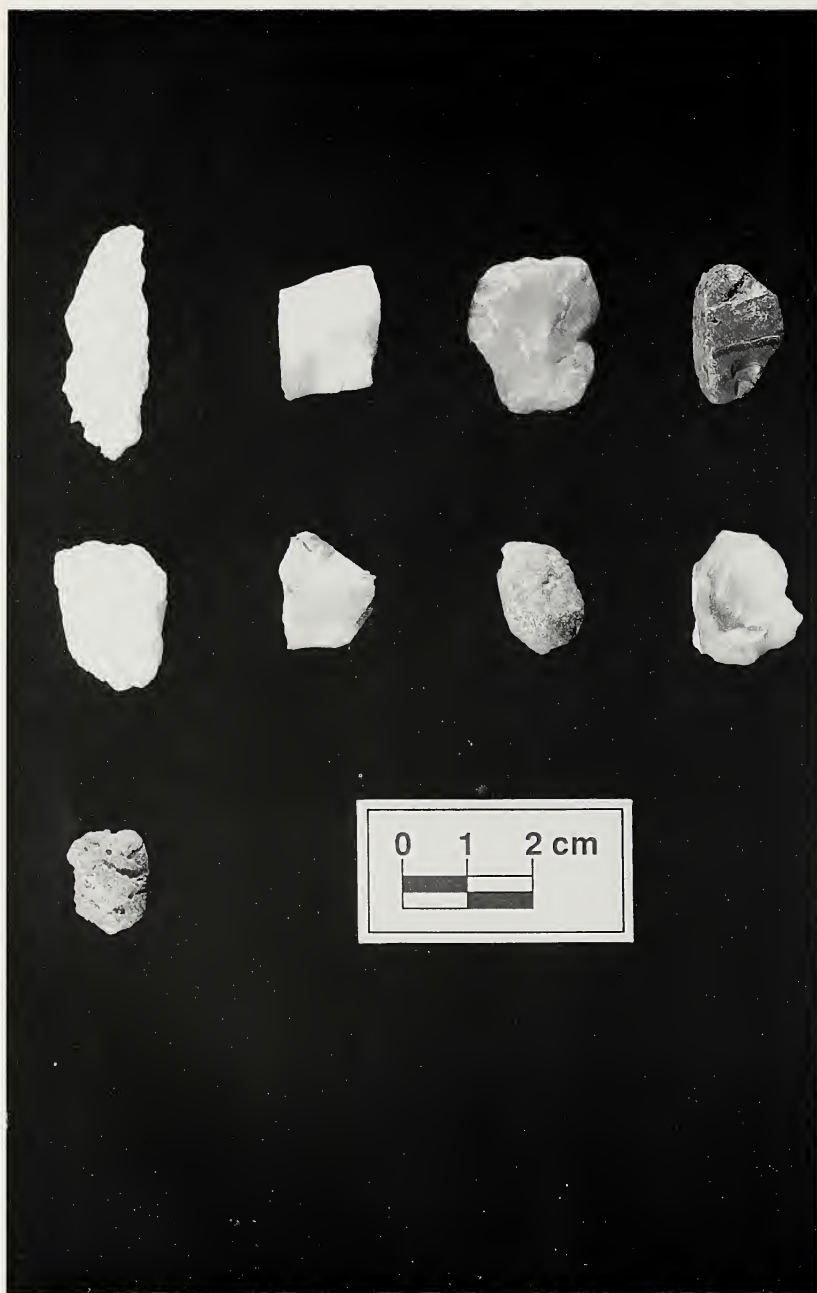


Fig. 13.—Well-shaped bead materials (Bead Preform 3) recovered from the Trants site (MS-G1), Montserrat.

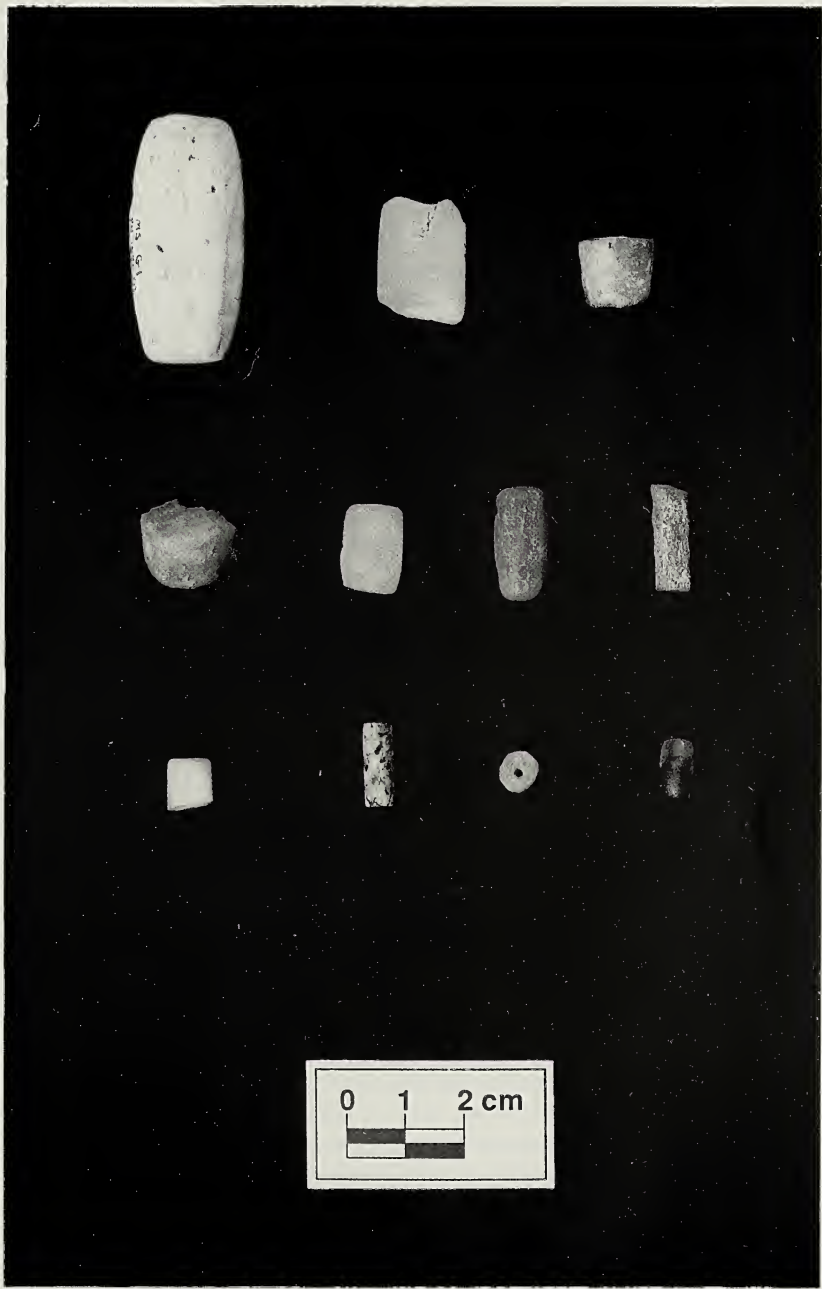


Fig. 14.—Fully shaped beads recovered from the Trants site (MS-G1), Montserrat.

product categories. In part, the results of their analysis indicate that manufacturing debris was not well represented in the Howes collection, which appears biased toward nearly finished and finished ornaments.

Saladoid Stone Bead Industries

Beads manufactured from exotic raw materials have been documented in Saladoid period contexts at many other sites in the Lesser and Greater Antilles; the closest source for many of the raw materials is mainland South America (Myers, 1981; Boomert, 1987). Stone bead manufacture seems to be less frequently represented in earlier preceramic, or later post-Saladoid contexts dated before and after the Saladoid period, respectively. Along with painted and incised ceramic wares, the stone bead industry and the extensive trade networks that supported it are an integral part of the Cedrosan Saladoid legacy (Rouse, 1992).

In addition to Trants, unequivocal evidence of on-site stone bead manufacture has been recorded at the Saladoid sites of Pearls in Grenada (Cody, 1990), Prosperity in St. Croix (Morse, 1989), and the related "Huecoid" site of Sorcé in Vieques (Chanlatte Baik, 1984). The notion of regional manufacturing centers and "ports of trade," originally proposed by Harrington (1924), has gained support as a result of more recent studies (e.g., Watters and Scaglione, 1994). Locating the sources of different exotic bead raw materials and accurately mapping their distribution remains a problem in the Caribbean, however (Cody, 1993).

Manufacture of certain bead materials, such as carnelian, appears to have been restricted to certain sites, like Trants, while the distribution of finished products was more widespread. Examples of finished beads are known from sites such as Hacienda Grande in Puerto Rico (Rouse and Alegría, 1990), Hope Estate in St. Martin (Haviser, 1991), Hichman's in Nevis (Wilson, 1989), Morel in Guadeloupe (Durand and Petijean Roget, 1991), Prosperity in St. Croix (Morse, 1989), the related "Huecoid" site of Sorcé in Vieques (Chanlatte Baik, 1984), and Vivé in Martinique (Mattioni, 1979), among many others. Stone beads and other ornaments provide some of the best evidence for the presence of an extensive maritime trade network during the Saladoid period (Watters, 1997).

The exchange of beads and ornaments manufactured from exotic materials and their inherent value is also well documented ethnographically and ethnohistorically. Their value was undoubtedly associated with the limited supply of exotic raw materials but also likely reflected the skill and labor involved in bead production. Flaking, pecking, grinding, and polishing likely were labor intensive tasks, but they probably were expedient relative to drilling. Roth (1924:79) writes of Guiana Amerindians producing quartz beads four to eight inches long, drilled lengthwise, a process purportedly taking up to two lifetimes to complete. To drill the beads, they apparently used pointed shoots of plaintain leaves, fine sand, and water (Roth, 1924:79). At the very least, such accounts provide some measure of the labor and equipment required to produce stone beads by hand.

Ethnographic accounts from lowland South America and ethnohistoric accounts of Taino trade record the exchange of exotic stones, particularly "greenstone," or nephrite (e.g., Lovén 1935; Myers 1981; Boomert, 1987). These long-range exchange networks, presumably with mainland South America, were in place throughout the entire Saladoid period based on the vertical distribution of bead manufacture materials at Trants. Manufacturing debris and finished beads were found in deeply stratified midden deposits which have been radiocarbon dated as

early as 480 B.C. \pm 80 (Beta-44828) at Trants (see Table 1). Bead specimens recovered from even deeper, but as yet undated, levels provide even earlier evidence of this Amerindian technology, some of the earliest evidence in the entire Caribbean and northeastern South America.

DISCUSSION

Flake Production

The expedient flake technology of the Saladoid period, although relatively simple and inconspicuous, represents a highly efficient method of lithic tool production. The inventory of flake tools recovered from the Trants site illustrates that this industry was an important part of, if not the sole purpose of, chert pebble and cobble reduction. Although documenting the production of grater board flakes is a more difficult matter, support for widespread production of grater boards among Saladoid people seems probable. Future studies may even show that manufacturing centers existed, with production localized at a few localities.

Unlike ceramics and crop cultivation, utilitarian flake production was not introduced to the Antilles by Saladoid populations. Earlier Archaic populations utilized flakes as makeshift tools long before, in addition to manufacturing blades and, less frequently, stemmed, projectile point-like bifaces. Utilized flakes have been documented in the same early, preceramic contexts as diagnostic blades and/or projectile point-like bifaces in Antigua (Nicholson, 1976a, Davis, 1993), St. Thomas (Bullen and Sleight, 1963; Lundberg, 1991), Puerto Rico (Ortiz, 1976; Pantel, 1988), Hispanola (Dávila, 1978; Ortega and Guerrero, 1985; Veloz Maggiolo, 1991), and Cuba (Kozlowski, 1974). These sites represent at least two definable cultural groups, the Ortoiroid in the Lesser Antilles and Puerto Rico, and the Casimiroid in the Greater Antilles (Rouse, 1992).

Given the presence of minimally modified and utilized flake tools in Archaic sites, the only major element of the Archaic flake tool kit missing from later Ceramic period sites are the well-developed and complex blade industries. While it may appear that this represents a regression in lithic technology, it more likely represents the result of different cultural adaptations and a greater emphasis on other industries after the Archaic period. For example, in characterizing the lithic assemblage among Monserrate period sites in Puerto Rico, Roe et al. (1990) suggest that "while essential continuities remain, the absence of a blade technology in these sites may be the consequence of a technical devolution," as groundstone was increasingly emphasized.

The need for well-made flake tools among the preceramic groups was not quite so pertinent for later Saladoid people either. Increased trade and a corresponding increase in the supply and variety of raw materials during the Saladoid period, as documented at Trants, suggest that the time invested in conservatively manufacturing modified flake blades or knives was unnecessary when the sharp edge of any number of the readily available unmodified flakes would suffice.

Raw material trade in the Antilles did not originate with ceramic-producing Saladoid peoples, however. Artifacts manufactured from exotic raw materials have been documented at some preceramic sites (e.g., Crock et al., 1995), and it is rather implausible that Archaic peoples acquired all of their material directly. Many earlier preceramic sites are located at or near chert sources (e.g., Kozlowski, 1974; Ortiz, 1976; Haviser, 1989:8), but Goodwin (1978:12) notes that this was not a prerequisite for Archaic period sites. In some cases Archaic populations

apparently did reduce raw materials at the source areas rather than at their habitation sites (Dávila, 1978), however, which is a different pattern than that observed at Trants and other Saladoid period sites.

The abundant source of lithic raw material at Long Island, Antigua, which dominates the lithic inventory at the Saladoid period Trants site, also was exploited by earlier Archaic populations (Davis, 1974, 1993). Long-term usage of this flint deposit by Amerindians resulted in one expansive quarry site which likely represents countless visits by groups and/or individuals seeking raw material. As noted by Olson (1973:101), there are: "tools, cores and chips strewn all over the place, by the tens of thousands—several acres literally covered with flint." Investigations of the Long Island source areas and quarry sites indicate that knappers employed a standardized reduction sequence geared toward the production of high quality cores for easy transport (Gijn, 1993). The repeated use of this particular locale over time makes it one of the most significant lithic raw material sources in the Lesser Antilles, at least for nonbead specimens.

The technologically basic tradition of simply produced utilized flakes continued from the preceramic, throughout the Saladoid period, and carried over into later Ceramic periods. Such tools are documented in collections from numerous post-Saladoid sites such as Blackman's Midden in Antigua (Nicholson, 1976*b*), Villa Taina in Puerto Rico (Goodwin and Walker, 1975), and in collections from several sites in Anguilla recently inventoried (Crock and Petersen, 1997). The continuity of this tradition, from the Archaic period onward throughout Amerindian prehistory, testifies to its suitability for West Indian environments.

Stone Bead Production

Analysis of Saladoid period stone bead manufacture at the local level, such as recently begun for the Trants site, indicates that bead production was a complicated process which required a higher level of technical proficiency than any other Saladoid period lithic industry. The skill and labor required for bead production certainly contributed to the significance of these ornaments to Amerindians as did the exotic nature of the raw materials used.

Saladoid bead manufacturing "centers" such as at Trants in Montserrat, Pearls in Grenada (Cody, 1993), and Sorcé in Vieques (Chanlatte Baik, 1984) provide strong support for specialization by individual villages in the production of beads of certain raw materials during the Saladoid period. It is evident that finished beads of these materials (i.e., carnelian and amethyst) occur at a greater variety of sites than does the evidence of their manufacture. This indicates that lapidaries at these manufacturing "centers" probably worked to satisfy both local and regional demands for certain types of beads.

Archaeological evidence and ethnographic analogy suggest that, once complete, the beads themselves likely symbolized status and/or rank. Finished beads representing a variety of raw materials were recovered in burial contexts at the Hacienda Grande (Rouse and Alegría, 1990), Morel (Durand and PetiJean Roget, 1991), and Vivé (Mattioni, 1979) sites. Such ceremonial associations, especially when associated only with certain burials, illustrate the use of stone bead ornaments to distinguish individuals, perhaps to signal status or rank. Among the ethnohistoric Taino of the Greater Antilles and some lowland South American groups, stone beads were highly valued signs of rank which reportedly were

passed down over generations (Lovén, 1935:478; Rouse, 1948b:553; Boomert, 1987:37).

Particular attention to the archaeological context of stone bead ornaments will lead to a better understanding of Saladoid period social organization given the roles these items played in communicating status, rank, or ideological information. At the regional level, the distribution of bead raw materials and finished beads provides the best available evidence for long-distance trade and exchange during the Saladoid period. The study of Saladoid period bead production is therefore critical, not only to the investigation of lithic technology during this period, but also to the study of Saladoid period socioeconomic systems.

CONCLUSIONS

As ceramic traditions evolved and changed, Saladoid period lithic technologies endured. Given the associations of flake production and bead manufacture with the earliest occupation of the Trants site, one of the earliest now known for the Ceramic period in the Caribbean, it is evident that both traditions were fully in place at the time of Saladoid colonization. At the same time Saladoid populations were adapting to local conditions by exploiting local resources such as Antigua chert, they continued to maintain a connection with mainland South America through trade in exotic bead materials such as amethyst and nephrite. The integrity of lithic industries throughout the Saladoid period helps document the successful adaptation of these mainland peoples who migrated to the Lesser Antilles and Puerto Rico.

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ON THE GENERIC STATUS OF *PALAEOPHICHTHYS PARVULUS*
EASTMAN 1908 AND *MONONGAHELA STENODONTA* LUND 1970
(OSTEICHTHYES: DIPNOI)

ANNE KEMP¹

ABSTRACT

The genus *Monongahela* Lund 1970, a species of dipnoan based on small tooth plates from the Duquesne limestone, Upper Pennsylvanian, in Mount Washington, Allegheny County, Pennsylvania, has been designated a junior synonym of *Palaeophichthys parvulus* Eastman 1908. Alternative interpretations of the material are, however, possible. *Palaeophichthys parvulus* is known from two juvenile specimens from the Francis Creek shale, Carbondale Formation, Middle Pennsylvanian, in the Mazon Creek area of Grundy County, Illinois. These are compressed, with macerated heads. The holotype has poorly preserved upper and lower tooth plates. Characters for comparison with *Monongahela* can be derived only from the upper tooth plates. None of the tooth plate characters that can be reliably distinguished in *P. parvulus* are sufficient to separate this species from a range of other lungfish genera, and both taxa are found at localities where other dipnoan genera occur. Because additional material and definition of all of the lungfish in the localities are needed to settle the question of congenerity of *Palaeophichthys* and *Monongahela*, separation of the two genera should be retained at present.

KEY WORDS: fish, *Palaeophichthys*, *Monongahela*, Carboniferous, Dipnoi

INTRODUCTION

Palaeophichthys parvulus is a problematic dipnoan taxon, described by Eastman (1908) on a small, poorly preserved specimen. A second specimen, slightly larger, was assigned to this species later (Eastman, 1917), but this material adds little information. Both specimens are compressed and have reasonable preservation of the body form and the squamation, but the heads are macerated. *Monongahela stenodonta*, described by Lund (1970), is a genus based on an extensive series of small tooth plates and jaw bones from a slightly younger locality. No skull bones or compressed fish are known for this genus. *Monongahela* has recently been made a junior synonym of *Palaeophichthys* (Schultze, 1994), an opinion based apparently on the existence in the holotype of *P. parvulus* of a single, partially preserved upper tooth plate that resembles the tooth plates described as *M. stenodonta*. Schultze (1994) has further described *P. parvulus* as a gnathorhizid, despite characterizing the skull roof as having a series of unpaired median bones.

Comparison of the two specimens of *P. parvulus* with tooth plates and body form in hatchlings of one species of a Recent lungfish, *Neoceratodus forsteri*, suggests that both specimens of *P. parvulus* are juvenile, as are the tooth plates belonging to *M. stenodonta*. Diagnosis of species on juvenile material is possible in a bradytelic group like lungfish, but none of the characters used by Schultze (1994) are reliable at generic or specific level. Consideration of both specimens of *P. parvulus* and comparison of the upper tooth plates with material from other

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genera, including specimens of *Sagenodus* cf. *S. periprion*, contemporaneous with *M. stenodonta*, suggests that synonymy is premature. Examination of available characters indicates that although *Palaeophichthys* and *Monongahela* are not congeneric, it is impossible at this stage to be sure of the true affinities of *P. parvulus*.

Specimen designations: CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; QM, Queensland Museum, South Brisbane, Queensland, Australia; USNM, National Museum of Natural History, Smithsonian Institution, Washington, D. C.

MATERIALS AND METHODS

Comparable Populations of Juvenile Dipnoans

A large sample of young *Neoceratodus forsteri*, collected as eggs from the Brisbane River in southeast Queensland and reared in the laboratory, including juvenile fish of stages 53–57 and isolated tooth plates of stages 54–57, has been used for comparison with the holotype and the hypotype of *P. parvulus* and with other fossil material. Stage 53 hatchlings are three months old and stage 57 hatchlings are nine months old. Growth and development of young stages of *N. forsteri* is described in Kemp (1982), and additional details are provided in the description below. Tooth plates and attached jaws of *M. stenodonta* came from the type locality of the Duquesne limestone (Lund, 1970). Additional juvenile specimens of *Sagenodus* cf. *S. periprion* from the same locality as *M. stenodonta* were used for an outgroup comparison. Specimens of this taxon provide the only possible outgroup comparison, not because they are necessarily appropriate in cladistic terms, but because this population is the only other large sample of juvenile fossil dipnoans that are less derived than *Monongahela* and *Palaeophichthys*.

Originals of the holotype and hypotype of *P. parvulus* have been examined in the National Museum of Natural History, Smithsonian Institution, Washington, D. C., and in the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, and compared with latex peels of the same specimens in the personal laboratory of Dr. D. Baird, Pittsburgh, Pennsylvania, and at the Museum of Natural History, University of Kansas at Lawrence. The holotype of *M. stenodonta* has been examined at Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, and a series of specimens were borrowed for more detailed comparison and analysis.

Scanning Electron Microscopy

Isolated tooth plates were mounted on stubs, coated in gold, and examined in a Phillips 505 scanning electron microscope.

Biometry

Measurements of lengths and breadths of the tooth plates and of the angles between the ridges were done by making a camera lucida drawing of the occlusal surface of each tooth plate, set level, and measuring angles and lengths on the drawing with a ruler and protractor. The enlargements of each specimen were the same in every case. Positions of the measurements of lengths, breadths, and angles taken are shown in Figure 1. Length of the tooth plate from the tip of ridge 1 to the tip of the last ridge is the dimension most suitable for tooth plates that are

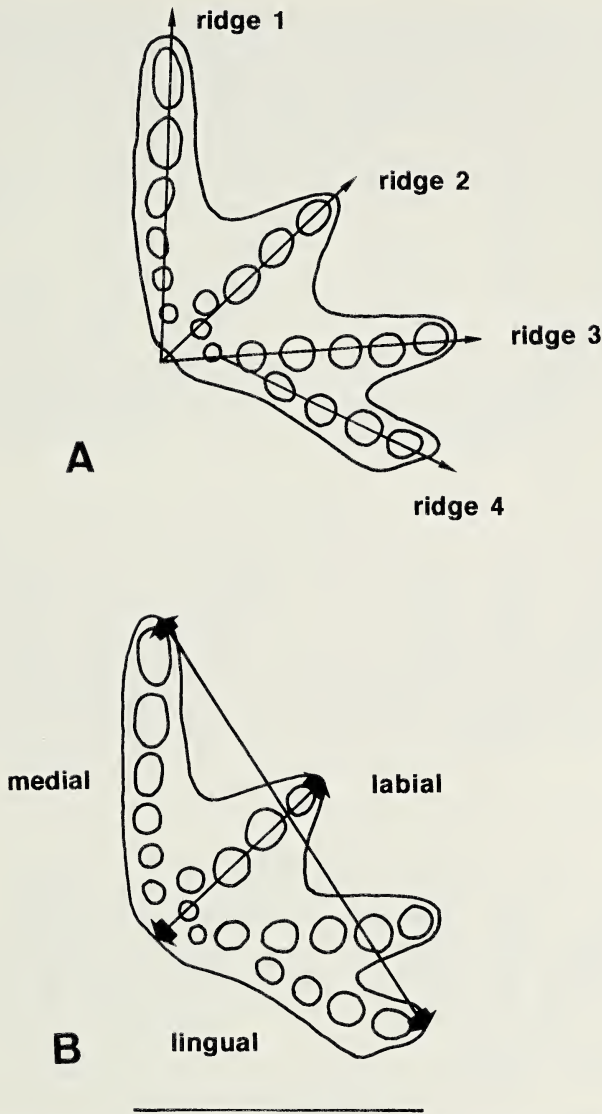


Fig. 1.—Measurements taken of tooth plates based on an upper tooth plate of *Neoceratodus forsteri* at stage 54, and terms used when describing tooth plates. A, angles between ridges; B, length and breadth. Scale bar = 1 mm.

still cusped. Breadth of the tooth plate is taken from the mediolingual junction to the tip of ridge 2. Angle measurements were done by fitting a straight line as closely as possible to the midpoints of each cusp. The ridges rarely meet in a point if the angles are drawn in this way, and further problems arise if the ridge is curved. However, the angles obtained for *M. stenodonta* are consistent with those obtained by Lund (1970, 1973), who used a different method.

Angles between the ridges of the upper tooth plate of *P. parvulus* are taken from Schultze (1994) and were also measured on his scanning electron micrograph

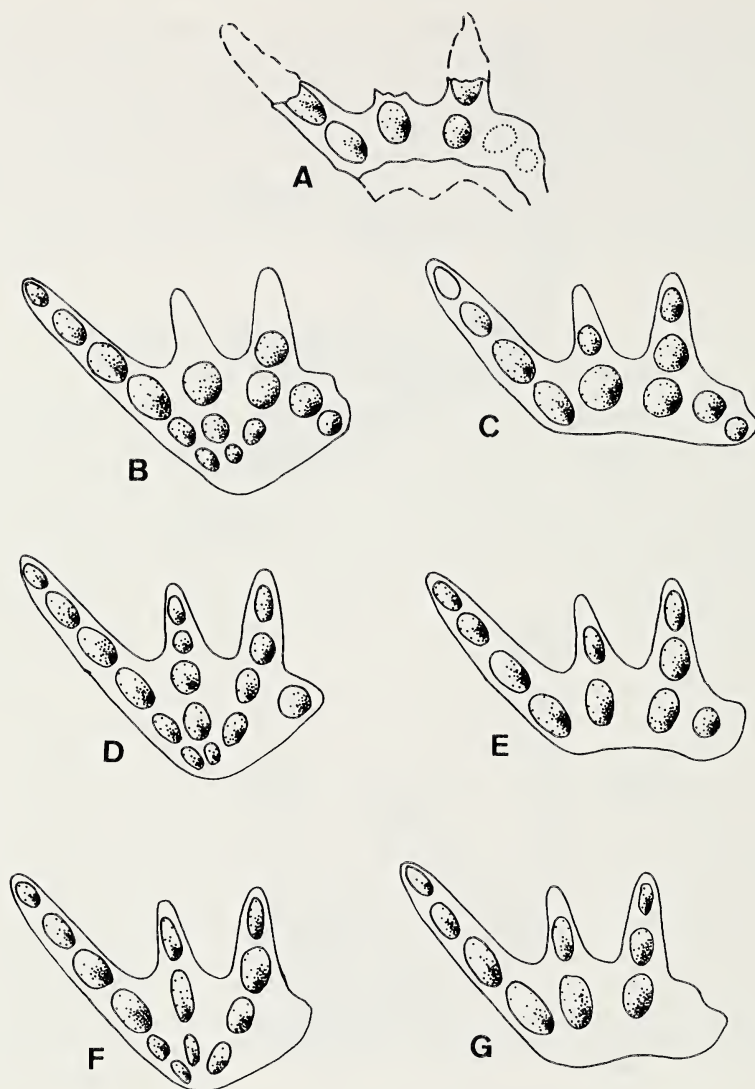


Fig. 2.—Drawings of the left pterygopalatine tooth plate of the holotype of *Palaeophichthys parvulus*. A, actual tooth plate drawn from the scan in Schultz (1994) and from latex peels; B, C, tooth plate reconstructed with five ridges; D, E, tooth plate reconstructed with four ridges; F, G, tooth plate reconstructed with three ridges. B, D, and F have ridges meeting in a point, with the medial portion of the tooth plate reconstructed. C, E, and G have no medial portion, and the tooth plates radiate from a line. Scale bar = 1 mm.

of the latex peel of the specimen (Fig. 2). Because measurements made on scanning electron micrographs require extensive correction before they can be accepted as accurate, these measurements of angles of *P. parvulus* are of value for descriptive purposes only.

Measurements of the lengths of the body and head of living *N. forsteri* hatch-

Table 1.—Characters used to determine the biological age of the specimens. 1 = squamation; 2 = calvarial bone development; 3 = articulation, calvarial bones; 4 = enamel cover; 5 = severity of wear on cusps; 6 = development of secondary denteons. See text for details.

Genus	Character					
	1	2	3	4	5	6
<i>Neoceratodus</i> stage 53	full	early	none	full	slight	none
<i>Neoceratodus</i> stage 55	full	partial	partial	full	slight	none
<i>Monongahela</i>	?	?	?	full	slight	none
<i>Palaeophichthys</i>	full	partial	partial	full	slight	none
<i>Sagenodus</i>	?	?	?	full	slight	none

lings, and the depth of head, body, and tail fin were done using calipers on anesthetized specimens. Measurements of the head and body of *P. parvulus* are taken from Schultze (1994).

Determination of the Biological Age of the Material

Biological age of a fossil specimen at death can be deduced from a number of characters by comparison with the juvenile, laboratory-reared material of known age from *N. forsteri*. Characters used to determine the age of the fossil species are squamation, degree of development and of articulation of the skull bones, enamel cover of the cusps, amount of wear on the cusps of the tooth plate, and the number of secondary denteons developed between the primary ridges. In the juvenile material of *N. forsteri*, these characters can be defined in full (Table 1). Only some can be determined for the fossil material.

Characters for Taxonomic Separation of Juvenile Dipnoans

Characters are modified from the lists used for adult lungfish in Kemp (1991a, 1992a, 1993a) and the characters used by Lund (1970, 1973). Some characters used on adult tooth plates and jaw bones were of no value for juveniles, as they have not yet developed, and others were too variable in young material. *Sagenodus* was used as the outgroup comparison. Characters are listed in the Appendix and explained below. The characters chosen apply for generic separation only, as *Palaeophichthys* is monotypic.

Character 1.—Shape of the upper symphysis is linear in *Sagenodus*. Other shapes, usually oval or half oval, are regarded as derived.

Character 2.—Shape of the lower symphysis is oval in *Sagenodus*, and other shapes, usually linear, are derived.

Character 3.—*Sagenodus* lacks an ascending pterygopalatine process for articulation with the dermal skull roof, but a process of variable shape is present on the pterygopalatine bone in the other genera examined.

Character 4.—Petrodentine, as defined by Lison (1941), is not common in dipnoans (Kemp, 1991b, 1992b; Lund et al., 1992). Absence of blocks of petrodentine in the tooth plates of juvenile lungfish is primitive, and its presence is derived (Kemp, 1995a). Small quantities of petrodentine may develop in older tooth plates of *Sagenodus* species, but this hard tissue is absent in juvenile *Sagenodus*.

Characters 5, 6, 7, and 8.—Shapes of ridge 1 and of the posterior ridges in each jaw are considered separately because they are not always the same. In the

upper tooth plate, curved ridges are primitive, and straight are derived. In the lower tooth plate, straight ridges are primitive, and curved ridges derived.

Characters 9, 10, and 11.—Most cusps in lungfish tooth plates show some compression, and this is often greater in the first ridge of a tooth plate compared to more posterior ridges. Compression is also more obvious in lower tooth plates. Slight lateral compression is regarded as primitive, and strong compression as derived.

Characters 12 and 13.—Ridge numbers in both upper and lower tooth plates vary according to growth and also show inherent variation. This character is often the same across a wide range of dipnoan genera, and to be useful, it must be defined with care. Juvenile tooth plates with more than five ridges in the upper jaw and more than four in the lower are primitive, and tooth plates with five ridges or less in the upper and four ridges or less in the lower are derived. This compromise applies only to juveniles in the genera considered here. Adult *N. forsteri* tooth plates have five or more ridges in both upper and lower jaws. Adult *Gnathorhiza* tooth plates have four ridges in the upper jaw and three in the lower. *Sagenodus periprion* has numerous ridges in each adult jaw.

Character 14.—Ridge 4 in the upper tooth plate, when present, may show the primitive condition, and begin level with ridge 3, at the mediolingual face, or start half way down ridge 3, independent of the mediolingual face. The latter character state is derived.

Characters 15 and 16.—In primitive dipnoans, the prearticular or pterygopalatine bone below the tooth plate extends beyond the dental tissues. In derived dipnoans, it follows the contours of the attached tooth plate.

Characters 17 and 18.—In primitive tooth plates, the ridges originate from a mediolingual line or curve. In derived specimens, the ridges of juvenile dipnoans originate approximately from a point situated medially or mediolingually.

SYSTEMATIC PALEONTOLOGY

Subclass Dipnoi Muller 1845

Family incertae sedis

Genus *Palaeophichthys* Eastman 1908

Synonym: None

- Palaeophichthys* Eastman, 1908:253, fig. 37.
Palaeophichthys Eastman, 1917:272, pl. 10, fig. 2.
Palaeophichthys Schevill, 1932:85.
Palaeophichthys Vorobyeva and Obruchev, 1964:314.
Palaeophichthys Romer, 1966:362.
Palaeophichthys Jessen, 1973:177.
Palaeophichthys Bardack, 1979:511.
Palaeophichthys Carroll, 1988:612.
Palaeophichthys Maples and Schultze, 1989:257, table 1.
Palaeophichthys Schultze, 1992:200.
Monongahela Schultze, 1992:201.
Palaeophichthys Schultze and Marshall, 1993:212.
Palaeophichthys Schultze, 1994:106–107.
Monongahela Schultze, 1994:107.

Amended Diagnosis.—Dipnoan with gracile and elongate body form; head short in relation to body; scales elongate, parallel sided, longitudinally striated with short, vermiculated free field; pterygopalatine tooth plate having straight radiating ridges with strong lateral compression of the cusps in the first ridge and

slight compression of the cusps in the second and subsequent ridges; prearticular tooth plate indeterminate.

Range.—Westphalian D, Upper Carboniferous.

Type Species.—*Palaeophichthys parvulus* Eastman 1908.

Palaeophichthys parvulus Eastman 1908

Palaeophichthys parvulus Eastman, 1908:253, fig. 37.

Palaeophichthys parvulus Eastman, 1917:272, pl.10, fig 2.

Palaeophichthys parvulus Schevill, 1932:85.

Palaeophichthys parvulus Vorobyeva and Obruchev, 1964:314.

Palaeophichthys parvulus Jessen, 1973:177.

Palaeophichthys parvulus Schultze, 1994:107.

Diagnosis.—As for genus.

Stratigraphic Position and Locality.—Francis Creek shale, Carbondale Formation, Middle Pennsylvanian (Westphalian D); Mazon Creek area, Grundy County, Illinois, USA.

Holotype.—MCZ 5090a, b, compressed fish with macerated head.

Hypotype.—USNM 4433, compressed fish with severely damaged head region.

Description.—*Palaeophichthys parvulus* is a dipnoan of slender and elongate shape. The head appears to be short in relation to the length of the body (14–15%) in both specimens, but because the full extent of the fleshy operculum is not preserved, the head may have been longer in the living fish. The tail is diphycercal, and the squamation well defined. The dentition is poorly preserved, and the only useful dental characters come from the pterygopalatine tooth plates. The right is represented by a lateral view of the first ridge only. The left appears to have three, four, or possibly five straight radiating ridges with strong lateral compression of the cusps in the first ridge and slight compression of the cusps in the second and subsequent ridges (Fig. 2A). Depending on the particular reconstruction used (Fig. 2B–G), ridge 4 may begin halfway down ridge 3, or may originate, like the other ridges, from a medial line or curve (Fig. 2B–G). The lower jaw is undiagnostic in both specimens. Despite the poor preservation, it is possible that there are three ridges in the prearticular tooth plate, but this is found in so many dipnoans, juvenile and adult, that it cannot be used for taxonomic determination. The fragment labelled as a vomer in Schultze (1994) has no characteristics of a vomer in the original specimen. It is present only as an impression, and alternative interpretations of this fragment are more probable, perhaps as one of the unidentifiable pieces of scattered and macerated skull bone.

In the holotype, the right pterygopalatine tooth plate is represented by three sharp, laterally flattened cusps of the first ridge, still covered to the tip in shiny brown enamel. No other ridges are visible. This appearance is consistent with any one of the species of small dipnoan contemporaneous with *Palaeophichthys* or *Monongahela*.

The left pterygopalatine tooth plate is represented by an impression, shown as a positive scan by Schultze (1994). Aside from the poor preservation, the mediolingual junction of the tooth plate is missing, as are the labial extremities of all the ridges. Traces of three ridges are present, as well as a probable fourth and a possible fifth (Fig. 2). Schultze (1994) has provided only one of several potential interpretations, and the characters displayed by the specimen are not entirely consistent with those of other dipnoan genera, even *Monongahela*.

One possibility is that five ridges are present (Fig. 2B, C). Ridge 1 has flattened cusps, ridges 2 and 3 have rounded cusps, ridge 4, with two rounded cusps begins in the middle of ridge 3, and ridge 5, with one cusp, has just begun to grow. It is possible that the ridges are long, straight, and acute, and radiate from a medial or posteromedial position (Fig. 2B). Alternatively, the ridges may radiate from a line or curve and may be short (Fig. 2C). The tooth plate may have only four ridges, the first long and straight with laterally flattened cusps, and the subsequent ridges shorter and also straight but with rounded cusps (Fig. 2D, E). The fourth may have begun to grow midway down ridge 3 (Fig. 2D), or all four ridges may radiate from a line or curve (Fig. 2E). It is also possible that only three long, straight ridges are present, radiating from a medial or posteromedial position, with the first long and straight with laterally flattened cusps, and the subsequent ridges shorter and also straight but with rounded cusps (Fig. 2F), or shorter, and radiating from a line or curve (Fig. 2G).

Comments.—Specimens of *Neoceratodus forsteri*, comparable in size with



Fig. 3.—Living hatchling of *Neoceratodus forsteri*. Scale bar = 1 cm.

those of *P. parvulus* (Fig. 3), are also slender and elongate. The head is long relative to the length of the body, 26–27%, but in the living juveniles considered for this paper, the head was measured to the back of the operculum, largely a fleshy structure in *N. forsteri*. The measurement of the head is, therefore, not strictly comparable in the two species. The pterygopalatine tooth plates that are commensurate in size with the tooth plate of *P. parvulus* have four straight ridges, with cusps in all ridges showing some slight lateral compression. In most upper tooth plates, ridge 4 begins midway down ridge 3 (Fig. 4A). Lower tooth plates are similar but have only three ridges at this age (Fig. 4B).

Comparable characters with the ability to discriminate generic status in *M. stenodonta* are the four radiating ridges in the pterygopalatine tooth plate, the first straight and the second and subsequent curved, all having cusps that are strongly compressed laterally (Fig. 4C, D). Cusps of ridge 4 begin to form midway down ridge 3. Lower tooth plates are similar, but have only three ridges. Characters of the body and head of this genus are not known. Vomerine teeth, however, have numerous small cusps (Lund, 1970).

Specimens of *Sagenodus* cf. *S. periprion* from the Duquesne limestones are known only from a number of upper and lower tooth plates with attached pterygopalatine and prearticular bones, all a little larger than *P. parvulus*. Pterygopalatine tooth plates have six or more curved ridges (Fig. 4E), and prearticular tooth plates have five or more straight ridges (Fig. 4F). Cusps of the first ridges show slight compression in both upper and lower tooth plates, and are short, rounded cones in the subsequent ridges, with the newest-formed cusp showing slight lateral compression (Fig. 4E, F).

In *N. forsteri*, *M. stenodonta*, and *P. parvulus*, ridges radiate roughly from a mediolingual point, and the angles are wide (Fig. 4, Appendix). In *S.* cf. *S. periprion*, angles are small, and the ridges radiate from a mediolingual line or curve (Fig. 4, Appendix).

Biological Age of the Specimens.—Characters for the assessment of the biological age of the specimens are listed in Table 1. Measurements of the head, tail, and body of *N. forsteri* juveniles, stages 53–57 (Kemp, 1982), are illustrated graphically in Figure 5, and mean angles between the ridges of upper and lower tooth plates are listed in Table 2. Corresponding available measurements of the angles between the ridges of *M. stenodonta* and *Sagenodus* cf. *S. periprion* specimens, as well as angles between the ridges of *P. parvulus*, are included in the

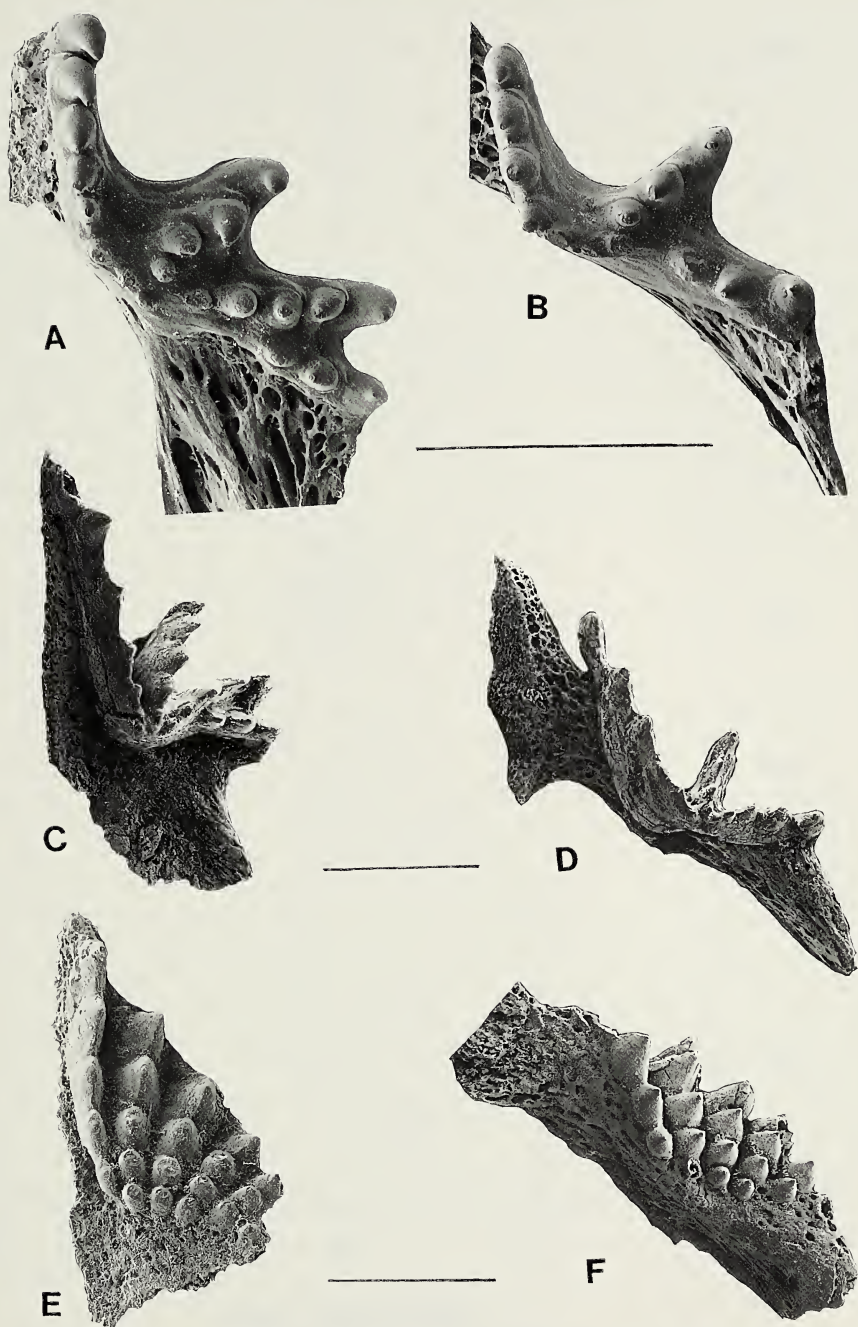


Fig. 4.—Scanning electron micrographs of juvenile lungfish tooth plates. A, B, *Neoceratodus forsteri*. A, upper tooth plate QM 26023; B, lower tooth plate, QM 26024. C, D, *Monongahela stenodonta*. C, upper tooth plate, CM 25633; D, lower tooth plate, CM 19415. E, F, *Sagenodus* cf. *S. periprion*, CM collection. E, upper tooth plate; F, lower tooth plate. Scale bars = 1 mm.

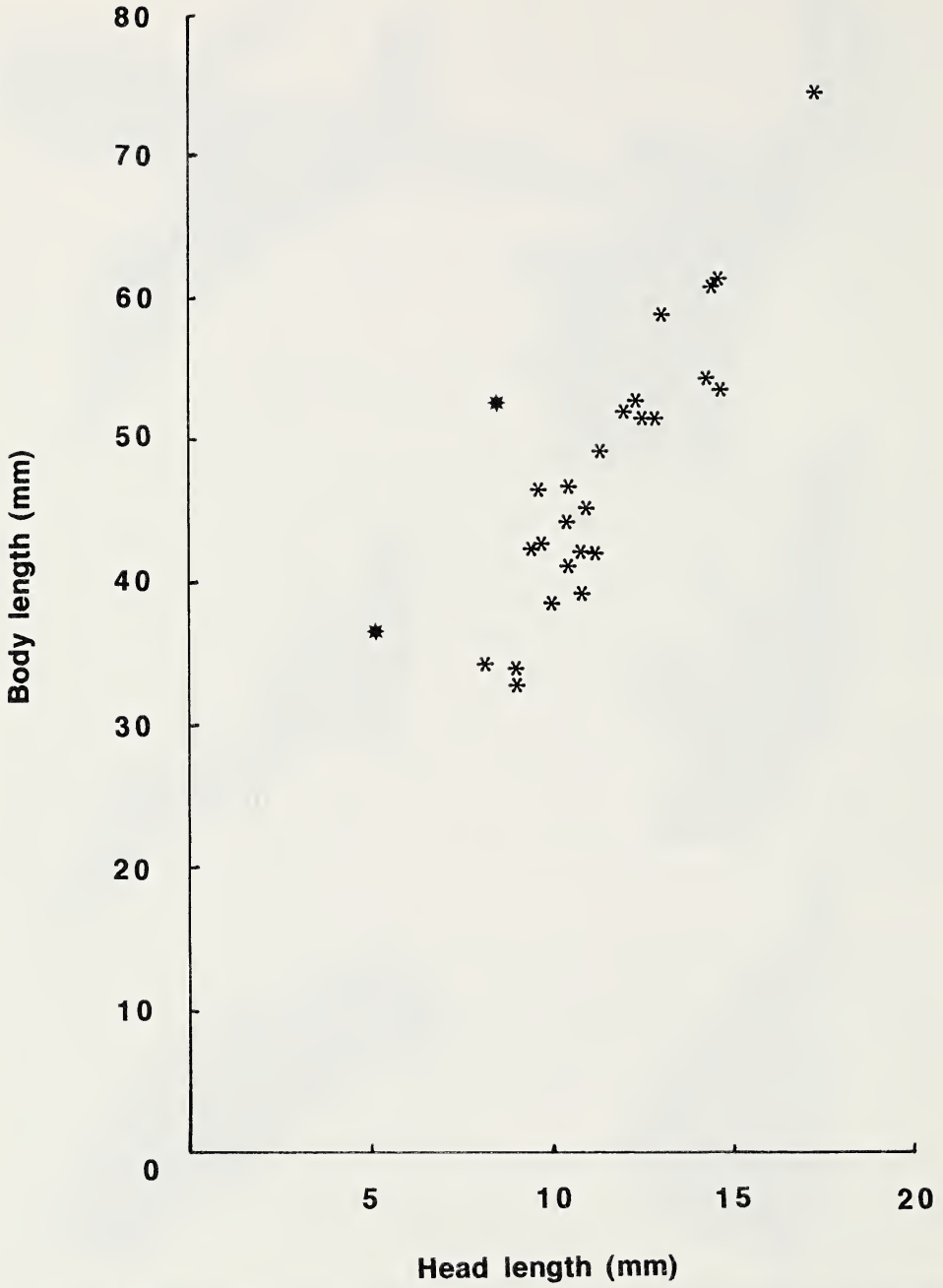


Fig. 5.—Graph showing body lengths of *N. forsteri*, with the sizes of *P. parvulus* material included. Asterisks represent the data for *N. forsteri* hatchlings, and stars the data for *P. parvulus* hatchlings.

Table 2.—Measurements of upper tooth plates of dipnoan species.

	Length	Angle, ridges 1–2	Angle, ridges 2–3	Angle, ridges 3–4	Angle, ridges 4–5
<i>Neoceratodus forsteri</i>	1.5 mm ± 0.3 mm	51.6° ± 5.6°	35.7° ± 5.0°	24.7° ± 6.34°	—
<i>Monongahela stenodonta</i>	2.6 mm ± 1.2 mm	40.4° ± 6.5°	40.2° ± 8.5°	31.2° ± 8.3°	—
<i>Sagenodus</i> cf. <i>S. periprion</i>	2.6 mm ± 1.2 mm	10.7° ± 2.9°	16.2° ± 5.1°	14.7° ± 5.7°	20.2° ± 5.1°
<i>Palaeophichthys parvulus</i>	1.2 mm ¹	40° ¹	28° ¹		
	1.2 mm ²	35°	24°	30°	23°

¹ From Schultz, 1994.

² Specimen incomplete, but would have been larger than 1.2 mm.

table. Relative dimensions of the body and head of *P. parvulus* are indicated in Figure 5.

Although the head of *P. parvulus* is apparently shorter in relation to the body compared with juvenile *N. forsteri*, the body form of both species is elongate. *Palaeophichthys parvulus* is more gracile than *N. forsteri*, but both specimens fit within the range of body lengths of *N. forsteri* juveniles (Fig. 5), with the holotype closest to stage 53 of *N. forsteri* and the hypotype closest to stage 55 (Fig. 5). The holotype of *P. parvulus* is 3.6 cm long and the body is 0.45 cm in depth (Schultze, 1994). The hypotype is slightly larger, 5.2 cm long and 0.7 cm in depth (Schultze, 1994).

The left upper tooth plate of *P. parvulus*, although not well preserved, displays the characters of many other small lungfish tooth plates. The few surviving cusps are separate and still distinct, and wear appears to be slight. None of the labial or the most medial cusps can be reliably assessed as the ridge tips and the medial face of the tooth plate are broken. There is no trace of the formation of additional dental tissues, represented by secondary denteons (punctations) that cause thickening of dental material between the ridges of the tooth plate. The right upper tooth plate, represented by three whole cusps of the first ridge, reveals that the enamel covering of the cusps reached the tips in this specimen. There is no sign of wear on the cusps. Squamation in both specimens is complete, extending as far as the head, and most of the calvarial, palatal, and mandibular bones appear to be present.

The macerated condition of the head in both specimens means that it is not possible to describe with any accuracy the pattern of the dermal skull roof or the cheek region of the holotype or the hypotype. Most of the bones have lost their original relationships, and the few that remain close together suggest one pattern in the holotype and another in the hypotype (Schultze, 1994). Articulation may not have been complete in either specimen.

As in both specimens of *P. parvulus*, a full set of squamation is present in *N. forsteri* from stage 53 onward (Kemp, 1982). At stage 53 in *N. forsteri* the larger calvarial bones have begun to form and to ossify but are not yet articulated with each other. The smaller calvarial bones have not appeared. Jaws are represented at stage 53 by well-ossified prearticular, articular, and pterygopalatine bones, and the parasphenoid, ceratohyal, and shoulder girdle are also mineralized. Articulations of palatal, mandibular, and shoulder girdle bones are forming. The vomer, positioned on the rostral cartilage of the chondrocranium, is also ossified, but never forms an articulation with any bone. At stage 55, most of the calvarial bones are present and anterior calvarial articulations have begun to form, although these are still incomplete, as is the process of ossification of the bones. The descending process of the anterior mediolateral bone, JLM in the nomenclature of Kemp (1992a), and the ascending process of the pterygopalatine bone are not yet fully articulated. The palate and lower jaw, with associated tooth plates, and the shoulder girdle are well ossified and firmly articulated.

The tooth plates of *N. forsteri* at stages 54–56 parallel exactly the structure of the smaller *M. stenodonta* and *Sagenodus* tooth plates, of comparable size, and the upper tooth plates of *P. parvulus*, as far as can be discerned (Fig. 2, 4). The cusps are clearly demarcated, and increase in size from the oldest, first-formed parts of the tooth plate to the youngest labial fringes. Each ridge has no more than six cusps, and each cusp shows little or no wear, even the medial cusps. In some specimens, a complete coat of enamel extends to the tip. Cusps can be

Table 3.—Data matrix for juvenile dipnoans, generic characters. Characters are listed in Appendix.

Genus		Character State			
<i>Sagenodus</i>	00000	00000	00000	000	
<i>Neoceratodus</i>	11100	01000	01111	111	
<i>Monongahela</i>	00111	00011	11111	111	
<i>Palaeophichthys</i>	????1	?1?0?	01?1?	???	

distinguished all the way to the mediolingual edge. There is no development of secondary denteons or thickening between the primary ridges. This appears much later, along with removal of cusps through wear, and the appearance of additional ridges and destructive removal of enamel and dentine from the mediolingual face of the tooth plate (Kemp, 1977, 1979).

All of the specimens of *M. stenodonta* fall within a narrow size range (Table 2). The smaller specimens, those comparable in size to *P. parvulus*, have characters consistent with those of other juvenile dipnoans (Fig. 4). Cusps are clearly demarcated, and grade in size from the smallest medial cusps to the largest labial cusps that have fused recently to the underlying bone base. The cusps are few in number, sharp, and show little wear. Where wear is present, it is restricted to the medial cusps. Secondary denteons have not yet appeared, and the ridges are cusped to the mediolingual face. These characters are evident in specimens of *S. cf. S. periprion* as well. Specimens of this species are slightly larger than those of *M. stenodonta*, but still have sharp conical cusps on each ridge, and all of the cusps are unworn. Posterior ridges with only one or two cusps indicate that the tooth plate was still growing actively at the time of death (Fig. 4E, F).

In larger *M. stenodonta* tooth plates, but not in *Sagenodus*, medial cusps show considerable wear, and labial cusps are still sharp. However, in both forms, none of the tooth plates show any development of secondary denteons, or thickening of tooth plate material, between the primary ridges of the tooth plate. The range of specimens available extends to material much larger than *P. parvulus*.

Angles between the Ridges.—The angles listed by Schultze (1994) as specific diagnostic characters of *P. parvulus* are 40° between ridges 1 and 2 and 28° between ridges 2 and 3. He does not give an angle for ridges 3 and 4. Angles measured on the scan by the methods used for other small lungfish in this work are 35°, 24°, 20°, and 18°, respectively (Table 2). Angles between the ridges of pterygopalatine tooth plates in *N. forsteri* and *M. stenodonta* are of comparable size (Table 2), and become progressively smaller in the posterior regions of the tooth plate, as in *P. parvulus*. Angles between ridges of *N. forsteri* are 51.6°, 35.7°, and 24.7° for ridges 1–2, 2–3, and 3–4 respectively (Table 2). Corresponding angles in *M. stenodonta* are 40.4°, 40.2°, and 31.2° (Table 2). Angles between the ridges of *S. cf. S. periprion* are much smaller and closer in size, 10.7°, 16.2°, 14.7°, and 20.2° for ridges 1–2, 2–3, 3–4, and 4–5 (Table 2).

Character Determination.—Character states for the species considered in this paper are given in the data matrix (Table 3). The reconstruction of *P. parvulus* that is closest to the interpretation of Schultze (1994) has been used for the determination of characters.

Cladistic analysis of these genera has not been performed because much of the data available for *N. forsteri*, *M. stenodonta*, and *S. cf. S. periprion* cannot be predicted or assumed for *P. parvulus*. The relevant parts of the specimen are missing, reducing the useful information to six characters (Table 3). An estimation

of phylogenetic relationships among the taxa considered here, based on the six characters and using *Sagenodus* as the outgroup, suggests that *P. parvulus* and *M. stenodonta* are both more derived than *N. forsteri*, but share few derived characters.

DISCUSSION

Ontogeny of *N. forsteri* is not always seen as relevant to the study of fossil dipnoan tooth plates (Campbell and Barwick, 1995), and it is certainly true that *N. forsteri* is not as closely related to *Monongahela* and *Gnathorhiza* as are the other Recent lungfishes, *Lepidosiren paradoxa* from South America, and species of *Protopterus* from Africa (Lund, 1970, 1973). Ontogeny of *N. forsteri* tooth plates is, however, better known than it is in lepidosirenids (Kerr, 1903, 1910; Kemp, 1977, 1979, 1992*b*, 1995*b*), and growth stages of *M. stenodonta* are comparable (Lund, 1970). Lepidosirenid lungfish also have tooth plates that are derived from the fusion of isolated cusps in radiating ridges, a form of development common in many lungfish, including *N. forsteri* (Kemp, 1995*b*). At the present state of our knowledge of lepidosirenid ontogeny, comparisons are limited to *N. forsteri*, and the juvenile tooth plates of this species are less different to those of *M. stenodonta* than they first appear to be. The ontogeny of *N. forsteri* is relevant to the study of fossil dipnoans, particularly the more derived of post-Paleozoic genera.

Small size does not necessarily mean that a fossil must have been or have come from a juvenile animal. It is not possible to be certain that a fossil known from limited material of minute size represents a juvenile animal or perhaps an adult, because a representative sample of life stages is rarely present. Criteria derived from comparison with living representatives of the group can be used instead to assess the biological age of a fossil at death. These can be drawn from body and head measurements, squamation, degree of development of skull bones, formation of firm articulations between skull bones, and a number of tooth plate characters, like the form of the cusps, their enamel cover, and the development of secondary denteons.

All of the fossil tooth plates examined for this study have the characteristics that define young *N. forsteri* of known stage of development and known biological age. Based on these criteria, it can be shown that *P. parvulus* and *M. stenodonta* specimens are the remains of juvenile fishes, and as such can be compared with the tooth plates of juvenile specimens of the Recent lungfish and with other juvenile fossil dipnoans, like specimens of *S. cf. S. periprion*. The specimens referred to *P. parvulus* and *M. stenodonta* are not as easily comparable with the tooth plates of adult lungfishes, including those of *Gnathorhiza*.

It is possible to discriminate species on juvenile material in a bradytelic group like lungfish, even if the only useful parts are tooth plates, provided that characters are chosen with care. This unfortunately leaves a restricted list. Many of the tooth plate characters used for discrimination among adult lungfish (Kemp, 1992*a*, 1993*a*), like the form of the prearticular sulcus, have not yet developed fully in hatchlings and juveniles. Other characters, like the origin of ridges, differ in juveniles and adults of the same species. In young *N. forsteri*, the three or four ridges are medial in origin, but in adults, with six or seven ridges, they are anterior in origin. (A medial origin for adult *N. forsteri*, stated in Kemp, 1993*a*:table 1, is a mistake.) Shapes in the jaw bones are not always useful. The form of the

jaw bone behind the tooth plate is often not preserved, and shows little variation. Most dipnoans have strong articular or quadrate processes on the prearticular and pterygopalatine bones, and the shapes are often similar. The same applies to the relationship between the first ridge and the symphysis. This is almost always parasymphyseal. Ridge length is not a reliable character either. In very young tooth plates, with only three or four cusps in a ridge, the addition of a single new cusp can make a large difference to the total length of the ridge.

The only points of comparison between *P. parvulus* and *M. stenodonta* are the preserved first ridge of the right pterygopalatine tooth plate and the imperfect impression of the left pterygopalatine tooth plate in the holotype of *P. parvulus*, and the large number of specimens of *M. stenodonta* tooth plates known. Generic identity has to be demonstrated on the upper tooth plates, as the only lower tooth plate present is too poorly preserved to distinguish any diagnostic characters. Examination of the few reliable characters indicates that separation of the two genera is appropriate, even using the reconstruction that is closest to the interpretation of Schultze (1994). Using any of the other possible reconstructions of the left pterygopalatine tooth plate of *P. parvulus* only serves to increase the differences between *P. parvulus* and *M. stenodonta*. This conclusion is, however, provisional, because reliable data are scarce.

Skull bones are not consistent between the holotype and hypotype of *P. parvulus*, and, apart from indicating that *P. parvulus* cannot be a gnathorhizid, have no impact on the question of synonymy with *M. stenodonta*. Species of *Gnathorhiza* and related genera all have a double C bone in the medial series (Berman, 1968, 1976, 1979; Olson and Daly, 1972; Kemp, 1993b). The few discernible postcranial features of *P. parvulus* are not particularly gnathorhizid in character. Juvenile gnathorhizids have been described as having a rounded eel-like body form, with a short, blunt tail and a head one-fifth of the body length (Dalquest, 1968). Using skull and body-form characters, *Palaeophichthys* is not a gnathorhizid.

There are at least six possible reconstructions of the upper tooth plate of *P. parvulus*. Each interpretation suggests different affinities for *P. parvulus*. It is possible that the tooth plate has five ridges, relating the hatchling to *Sagenodus* or to one of the undescribed species of dipnoan from either locality. It can also be interpreted as having three ridges. A small number of radiating ridges in a young fossil tooth plate, with cusps entirely covered in enamel and no secondary denteons present, is not uncommon. Equivalent characters are found in young *Megapleuron zangleri* (Schultze, 1977), a species occurring in Pennsylvanian deposits in North America, and in many other post-Paleozoic dipnoans, including *N. forsteri*. A third possibility is that it has four ridges, with the fourth ridge originating midway down the third. Joining of the fourth ridge on to the third lateral to the apex of the tooth plate is found in young *Gnathorhiza* as well as in *M. stenodonta*, a large proportion of small *N. forsteri*, and doubtless other dipnoans. Since the apex is missing, all the ridges, three, four, or five, could meet in a point, as is common in young *N. forsteri* and in *M. stenodonta*, or join a line or curve as in young *Sagenodus*.

Schultze (1994) has given a specific diagnosis of *P. parvulus* based entirely on the angles between ridges, and his measurements fall within the range of angles found in *M. stenodonta* (Lund, 1970, 1973; Schultze, 1994). Angles between the ridges are only valid as taxonomic determinants if based on a large statistical sample (Vorobyeva, 1967; Kemp, 1977). They should be measured on well-pre-

served and preferably original tooth plates, and care should be taken to distinguish the growth angles from the wear angles. Angles also vary among individuals of one species and between juvenile and adult specimens of the same species (Kemp, 1977). Variability is obvious in all of the species measured on tooth plates in this study. Because a diagnosis is intended to characterize a species or a genus to the exclusion of others, beyond reasonable doubt, angles do not have any validity measured on a cast of a single juvenile tooth plate.

Vomerine tooth plates of most post-Paleozoic dipnoans resemble a single ridge of the more complex prearticular and pterygopalatine tooth plates, and have cusps at the actively growing labial end. This is true even in large, old specimens. If the structure identified as a vomerine tooth plate by Schultze (1994) is a vomerine tooth plate, the lack of cusps is, firstly, most unusual and, secondly, a significant point of difference with *M. stenodonta*. This species has numerous minute cusps on the vomerine tooth plate (Lund, 1970).

The deposit from which *P. parvulus* was obtained contains at least three other species of lungfish (Lund, 1975, 1976; Hook and Baird, 1986, 1993). One of these, *Conchopoma*, differs fundamentally in skull and tooth-plate characters from most other post-Paleozoic dipnoans (Hook and Baird, 1993), and can be excluded as a genus that is close to *Monongahela* or *Palaeophichthys*. The deposit from which *Monongahela* came also contains other species of lungfish (Lund, 1970, 1973, 1975, 1976). None of these dipnoans is perfectly preserved and none can be characterized completely. *Palaeophichthys* is best classified as incertae sedis, a monotypic genus of uncertain affinities based on incomplete juvenile material. It is unlikely to be closely related to *Gnathorhiza* because it has an unpaired median C bone in the dermal skull roof (Schultze, 1994). *Monongahela* is a genus with close relationships to *Gnathorhiza*, and is known from an extensive series of dental material and attached jaws (Lund, 1970, 1973). Our knowledge of all of these species is incomplete, and *Monongahela* should not be regarded as a junior synonym of *Palaeophichthys*. Additional studies of all of these lungfishes are needed to decide questions of generic status.

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APPENDIX

Character Descriptions

The characters in the following list were used to assess the Recent and fossil tooth plates from juvenile dipnoans. Characters that could be determined on *Palaeophichthys parvulus*, marked with an asterisk, were too few to permit a cladistic analysis of the groups. Primitive states for each character are coded as "0" and determined from the condition of the outgroup, *Sagenodus*. The derived state is coded as "1."

1. Upper symphysis linear (0), upper symphysis not linear (1).
2. Lower symphysis oval (0), lower symphysis not oval (1).
3. Ascending pterygopalatine process absent (0), ascending pterygopalatine process present (1).
4. Petrodentine absent (0), petrodentine present (1).
- *5. Ridge 1 (upper) curved (0), ridge 1 (upper) straight (1).
6. Ridge 1 (lower) straight (0), ridge 1 (lower) curved (1).
- *7. Posterior ridges (upper) curved (0), posterior ridges (upper) straight (1).
8. Posterior ridges (lower) straight (0), posterior ridges (lower) curved (1).
- *9. Cusps of ridge 1 (upper) show slight lateral compression (0), cusps of ridge 1 (upper) show strong lateral compression (1).
10. Cusps of ridge 1 (lower) show slight lateral compression (0), cusps of ridge 1 (lower) show strong lateral compression (1).
- *11. Cusps of posterior ridges show slight lateral compression (0), cusps of posterior ridges show strong lateral compression (1).
- *12. Five ridges or more in upper jaw (0), fewer than five ridges in upper jaw (1).

* Data available from *P. parvulus*, using the interpretation of Schultze (1994) and the reconstruction of Figure 2D.

13. Four ridges or more in lower jaw (0), fewer than four ridges in lower jaw (1).
- *14. Ridge 4 (upper) begins level with ridge 3 (0), ridge 4 (upper) begins midway down ridge 3 (1).
15. Pterygopalatine bone extends beyond dentine ridges (0), pterygopalatine bone follows line of dentine ridges (1).
16. Prearticular bone extends beyond dentine ridges (0), prearticular bone follows line of dentine ridges (1).
17. Upper ridges radiate from a mediolingual line (0), upper ridges radiate from a mediolingual point (1).
18. Lower ridges radiate from a mediolingual line (0), lower ridges radiate from a mediolingual point (1).

REVISION OF THE NEOTROPICAL GENUS *ISCHYOMIUS*
WITH A DISCUSSION ON ITS SYSTEMATIC POSITION
(INSECTA: COLEOPTERA: TENEBRIONOIDEA: PYTHIDAE)

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ABSTRACT

The Neotropical genus *Ischyomius* Chevrolat is reviewed and comprises six species: *I. singularis* Chevrolat, *I. denticollis* Champion, *I. chevrolati* Champion, *I. bicolor* Champion, *I. nevermanni*, new species (Costa Rica, Limón Province), and *I. championi*, new species (Ecuador, Pichincha Province). The following new synonymies are proposed: *Pseudoischyomius* Pic 1923 = *Ischyomius* Chevrolat 1878; *Pseudoischyomius rufipennis* Pic 1923 = *Ischyomius bicolor* Champion 1916. Primary types were examined for all species, and lectotypes are designated for *I. singularis* and *I. chevrolati*. The systematic placement of *Ischyomius* is discussed, and based on structure of male and female genitalia, the genus is placed in the family Pythidae, provisionally near *Sphalma* Horn.

KEY WORDS: insects, Coleoptera, Tenebrionoidea, Pythidae (*Ischyomius*), Neotropics

INTRODUCTION

The Neotropical genus *Ischyomius* Chevrolat, like other enigmatic taxa within Tenebrionoidea, never has had a stable family placement. The genus was described by Chevrolat (1878) in Tenebrionidae, near *Acropteron* Perty. Champion (1886) retained this position, and created the "Ischyomiides," stating that many features of *Ischyomius* differed significantly from *Acropteron* and other tenebrionids. Later, Champion (1889) transferred *Ischyomius* to Melandryidae, based on possession of open procoxal cavities. This new placement was reflected in Champion's (1916) treatment of Melandryidae, in which *Ischyomius* is placed in the Ischyomiina, after the genus *Synchroa* Newman. Beginning with Csiki (1924), *Ischyomius* was placed in the Tetratominae (Melandryidae), near *Synchroa*. This was followed by Blackwelder (1945), Crowson (1955) as Tetratomidae, and Arnett (1983). Lawrence (1982) placed the genus in Pythidae without explanation, but stated that it was a very distinct group. Watt (1987) moved *Ischyomius* into Trictenotomidae based on adult similarities exhibited between the two taxa. Pollock (1994) stated, in the absence of detailed analyses, that *Ischyomius* belonged in Pythidae, based on structural similarities in male and female genitalia. This hypothesis was adopted by Pollock and Lawrence (1995). Lawrence and Newton (1995) treated the genus as Pythidae, incertae sedis.

This paper presents a taxonomic revision of *Ischyomius*, in which evidence is presented for the placement of the genus in Pythidae, provisionally near *Sphalma* Horn.

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MATERIALS AND METHODS

Collection abbreviations used in the text are: AAAC, Albert A. Allen collection, Boise, Idaho; BMNH, The Natural History Museum, London, United Kingdom; CASC, California Academy of Sciences, San Francisco, California; CMNH, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; CNC, Canadian National Collection of Insects, Ottawa, Ontario, Canada; DAPC, Darren A. Pollock private collection, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; FMNH, Field Museum of Natural History, Chicago, Illinois; FSCA, Florida State Collection of Arthropods, Gainesville, Florida; INBC, Instituto Nacional de Biodiversidad (INBio), Heredia, Costa Rica; MNHN, Entomologie, Muséum National d'Histoire Naturelle, Paris, France; MUCR, Museo de Insectos, Universidad de Costa Rica, Ciudad Universitaria, Costa Rica; NMNH, National Museum of Natural History, Smithsonian Institution, Washington, D. C.; OXUM, Hope Entomological Collections, Oxford University Museum, Oxford, United Kingdom; RHTC, Robert H. Turnbow, Jr. Collection, Fort Rucker, Alabama; SEMC, Snow Museum, University of Kansas, Lawrence, Kansas; SMTD, Staatliches Museum für Tierkunde, Dresden, Germany.

The techniques used for specimen preparation and study are the same as those explained in Pollock (1995). Type specimens were examined for all species of *Ischyomius*; label data are enclosed in quotes and individual labels are separated by a slash (/). Measurements are presented in millimeters, as follows: HL—length of head between anterior margin of labrum and anterior margin of pronotum; GHW—maximum width around head, across eyes; PL—length of pronotum along midline; GPW—maximum width across pronotum; EL—length of elytron from humerus to apex of spine; GEW—maximum width across both elytra; TL—sum of HL and PL and EL.

TAXONOMIC ACCOUNTS

Genus *Ischyomius* Chevrolat, 1878

Ischyomius Chevrolat, 1878:98; Champion, 1886:258; Champion, 1893:548; Champion, 1916:81; Seidlitz, 1916:387; Seidlitz, 1917:88 (as *Ischiomius*); Csiki, 1924:6; Blackwelder, 1945:494; Crowson, 1955:113, 132; Lawrence, 1982:544; Arnett, 1983:2; Watt, 1987:115; Pollock, 1994:522; Pollock and Lawrence, 1995:466, 468; Lawrence and Newton, 1995:897. Type species, *Ischyomius singularis* Chevrolat, by monotypy.
Pseudoischyomius Pic, 1923:21; Blackwelder, 1945:494. Type species, *Pseudoischyomius rufipennis* Pic, by monotypy. New synonymy.

Diagnosis.—Specimens of *Ischyomius* may be distinguished from other genera of Pythidae based on the following character states (also see key in Pollock and Lawrence [1995]): mandibles with lateral flange (Fig. 2A, D); pronotum wide, at least indistinctly explanate laterally, with distinct lateral carina; tarsomeres 1–4 (1–3 on hind legs) lobed (Fig. 3D), densely setose ventrally; elytra widest anteriorly, distinctly tapered posteriorly (Fig. 1).

Description.—Body (Fig. 1) elongate (TL/GEW 3.5–4.3), flattened slightly dorsoventrally, widest anteriorly and narrowed posteriorly; TL 5.9–13.4; GEW 1.5–3.8.

Head relatively short and wide, narrowed behind eyes; eyes large, relatively coarsely faceted, emarginate slightly near antennal insertions; frontoclypeal suture indicated laterally, medially marked by transversely sunken area; labrum transverse, anterior margin slightly emarginate to truncate; antennae elongate, antennomeres subserrate to filiform, slightly to moderately flattened. Mandibles (Fig. 2, 3B) large, prominent, slightly asymmetrical; apices unidentate, with small ventral accessory tooth situated posterior of apex; ventral lateral flange distinct, extended from accessory tooth to basal point of articulation; terebral teeth (Fig. 2E:t) short, blunt; both mandibles with dorsal carina (Fig. 2D:dc),

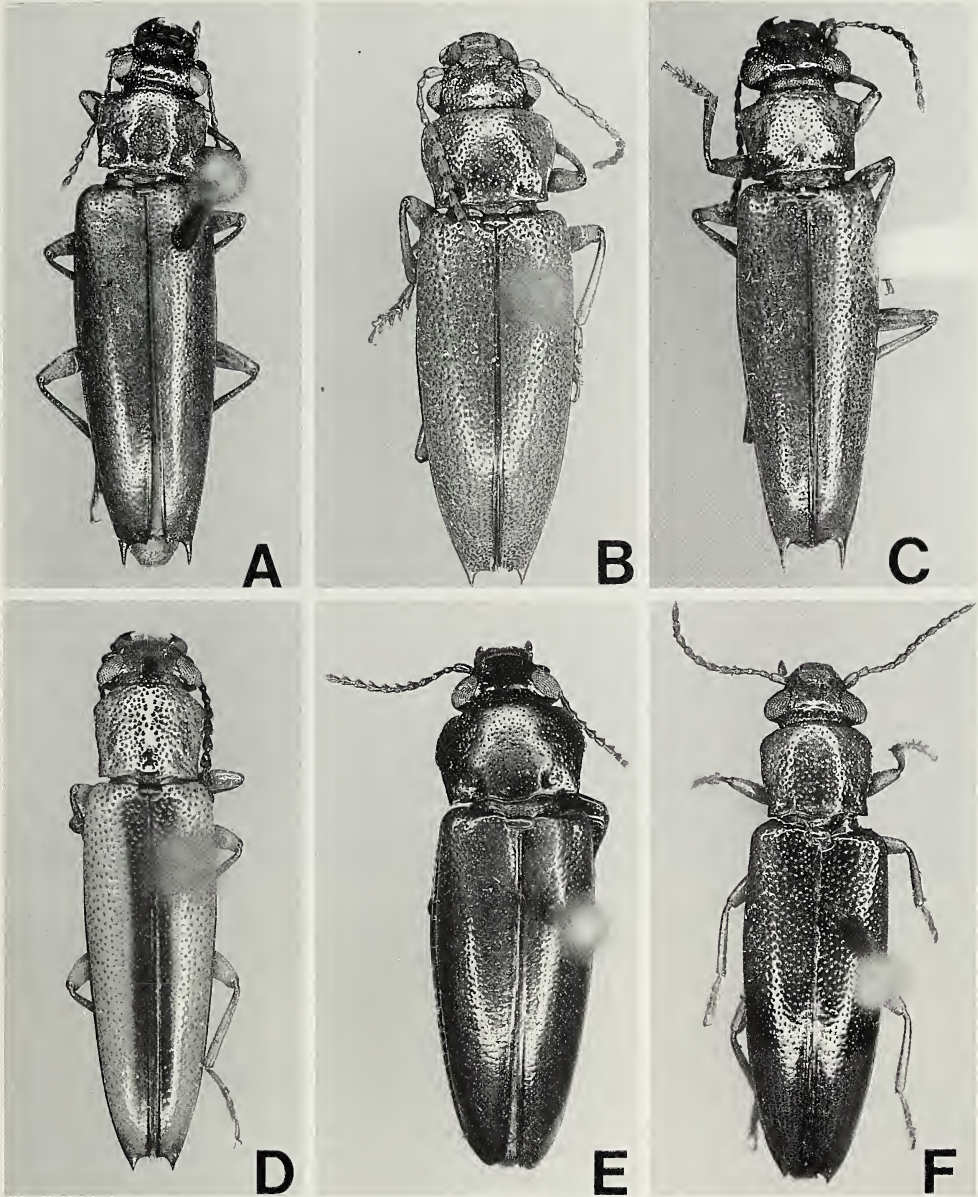


Fig. 1.—Dorsal habitus of *Ischyomius* species. A, *I. singularis* Chevrolat (TL 11.7 mm); B, *I. chevrolati* Champion (TL 9.9 mm); C, *I. denticollis* Champion (TL 10.1 mm); D, *I. championi*, n. sp. (TL 9.5 mm); E, *I. bicolor* Champion (TL 10.6 mm); F, *I. nevermanni*, n. sp. (TL 8.7 mm).

significantly more distinct on right mandible; ventral microtrichia (Fig. 2B:mi) elongate, extended posteriorly onto distinct prostheca (Fig. 2F:p); mola (Fig. 2C:m; 3B) distinct, subtriangular, concave and convex on left and right mandible, respectively; occlusal surface of mola composed of rows of minute asperities. Maxilla with large, subtriangular galea, fringed with dense, fine setae; lacinia reduced in size, fringed apically with long setae; apical maxillary palpomere securiform (Fig. 3A). Mentum (Fig. 3A) distinctly transverse, anterior margin evenly arcuate or slightly lobed; distinct pit

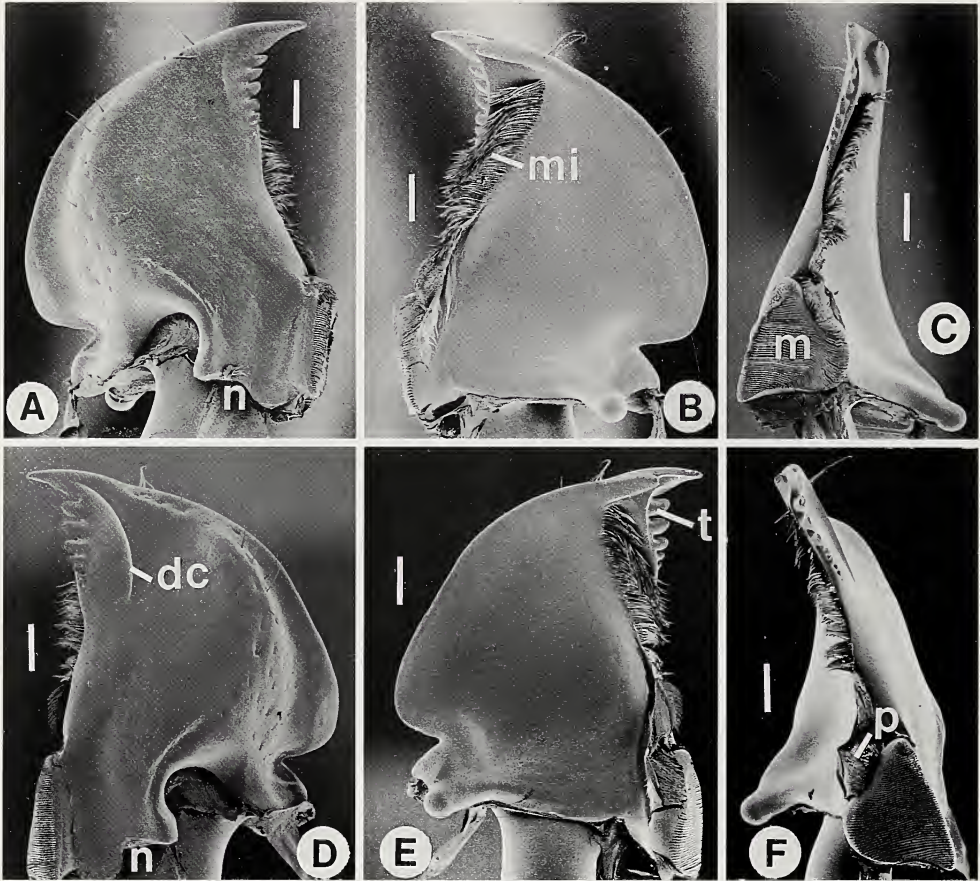


Fig. 2.—Mandibles of adult *Ischyomius chevrolati*. A, left mandible, dorsal; B, left mandible, ventral; C, left mandible, occlusal; D, right mandible, dorsal; E, right mandible, ventral; F, right mandible, occlusal. dc = dorsal carina, m = mola, mi = microtrichia, n = basal notch, p = prostheca, t = terebral tooth. Scale bar = 0.1 mm.

(Fig. 3A:p) in mentum in males of two species. Labium with apical palpomere similar in shape to maxillary palp, slightly securiform (Fig. 3A).

Prothorax wider than long, widest anteriorly; pronotal disc slightly and more or less evenly convex, with small depressions posterolaterally; disc slightly explanate laterally in one species (*I. singularis*); lateral edge of pronotal disc smooth (Fig. 4C) or with small tubercles (Fig. 4A); lateral pronotal carina distinct along entire lateral margin; posterior pronotal margin with or without distinct bead, at least vaguely bisinuate; prosternum anterior of coxae distinct; prosternal process (Fig. 3C) distinctly produced posteriorly between coxae; apex of process broadly rounded and margined; procoxae rounded, not extending significantly below process; procoxal cavities open externally and internally; protrochantins concealed.

Elytra elongate (Fig. 1), about 2.3–2.8 times longer than wide; sides subparallel anteriorly, then narrowed posteriorly; lateral margins visible dorsally or narrowly concealed; humeri distinct; disc evenly convex; epipleuron distinct, wide anteriorly, narrowed posteriorly, traceable to, or just anterior of, apical spine; apex of elytra with variously acute spine, indistinct in one species; scutellum transverse, broadly rounded posteriorly; mesosternum narrowly separating mesepisterna, sloping from anterior margin to intercoxal process; mesocoxae separated narrowly, trochantin concealed or barely visible between lateral extensions of meso- and metasternum; mesocoxal cavities closed partly by mesepimeron; metasternum convex, without distinct median line; metendosternite (Fig. 6) with mod-

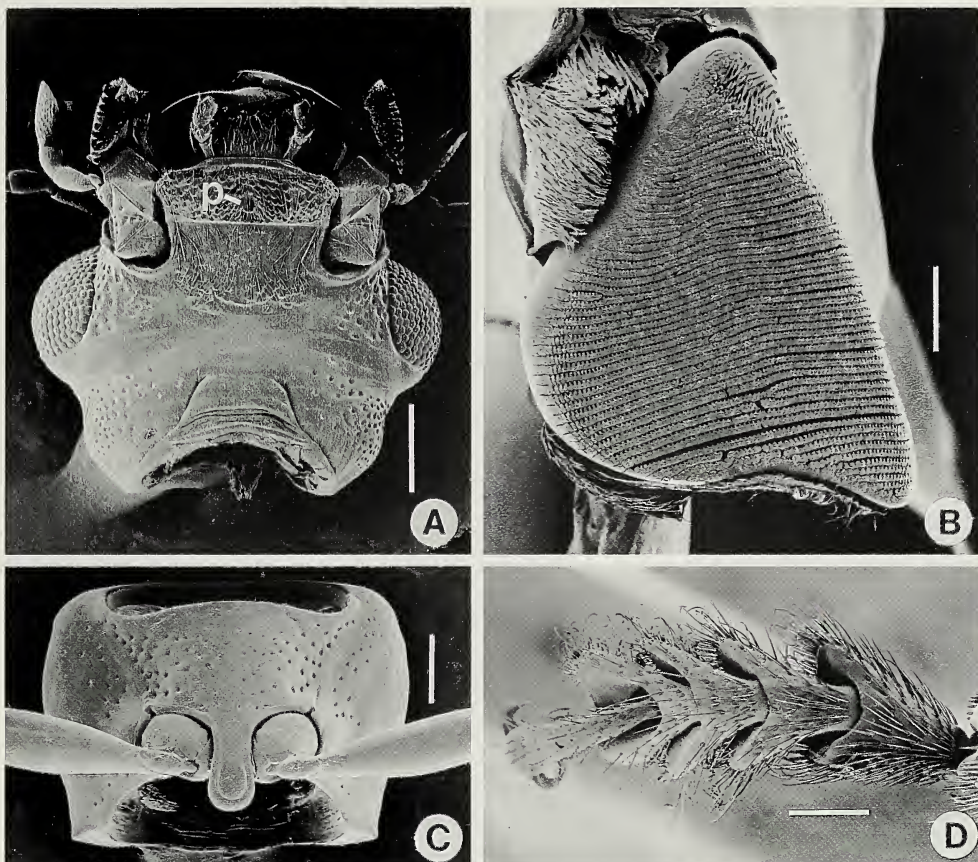


Fig. 3.—Structural features of adult *Ischyomius* spp. A, *I. singularis*, head, ventral view; B, *I. chevrolati*, detail of right mandibular mola; C, *I. chevrolati*, prothorax, ventral view; D, *I. singularis*, foretarsus, dorsal view. p = mental pit. Scale bar = 0.5 mm (A), 0.05 mm (B), 0.4 mm (C), 0.2 mm (D).

erately long, broad stalk; anterior tendons inserted on elongate arms distal of midlength; laminae broad, rounded laterally.

Hind wing (Fig. 5) with relatively short membrane; veins indistinctly pigmented (shown dark in figure for clarity); area beyond radial cell about 0.3 times as long as entire wing; radial cell distinct, small; medial region with four terminal veins; wedge cell narrow, elongate.

Legs slender, femora expanded slightly toward midlength; tibiae very slightly widened apically; apex of tibiae with row of stout setae; tibial spurs short, stout; inner apical surface of tibia with moderately dense brush of setae, especially distinct on fore tibiae; all but last tarsomere expanded laterally, triangular; tarsomeres (Fig. 3D) distally slightly emarginate, ventral surface with dense setae; apical tarsomere narrow, relatively elongate; tarsal claws relatively long and slender.

Abdomen with all segments freely articulated; ventral surfaces more or less uniformly punctate, with or without setae; tergite 8 broadly rounded apically; tergite 8 shallowly, broadly rounded apically; sternite 8 shallowly emarginate; sternite 9 in males with elongate spiculum gastrale.

Aedeagus (Fig. 7, 8B) with tegmen oriented dorsad of median lobe; basale subequal in length to apicale, or with apicale distinctly longer than basale; apicale variously narrowed to near apex, cleft slightly; accessory lobes short and angular, to slender and elongate, rounded or slightly spatulate distally, with setae basally and apically; parameral struts present, membranous towards, and articulated with, base of median lobe; median lobe parallel-sided, slender, apex evenly tapered, distinctly sclerotized along lateral margins only; tegmenite distinct, subquadrate, adpressed tightly against basale.

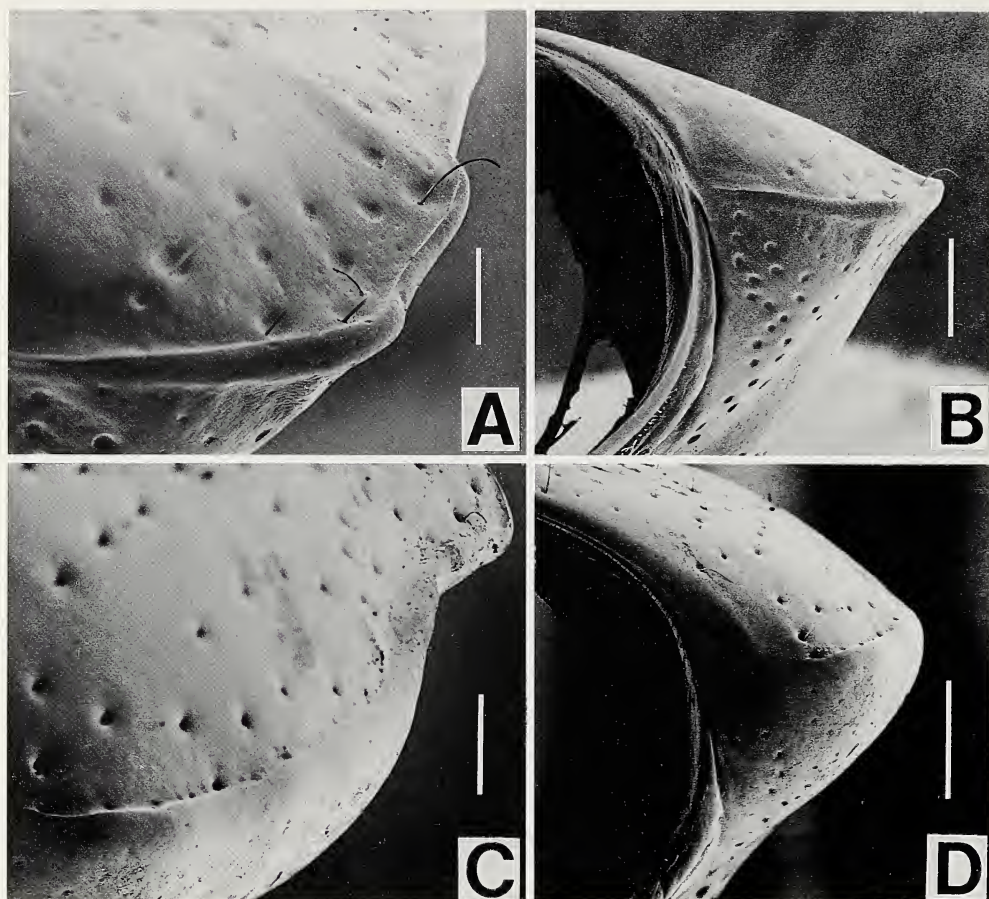


Fig. 4.—Prothoraces of *Ischyomius* spp. A, *I. singularis*, pronotal disc, anterolateral oblique view; B, *I. singularis*, prothorax, anterior view; C, *I. chevrolati*, pronotal disc, anterolateral oblique view; D, *I. chevrolati*, prothorax, anterior view. Scale bar = 0.1 mm (A, C), 0.2 mm (B, D).

Ovipositor (Fig. 8A) elongate, flexible; coxites three-segmented, apical segment distinctly longer than basal two; coxites sparsely setose, more so distally; two pairs of elongate baculi distinct; spiculum ventrale elongate, subequal or slightly greater in length than ovipositor; styli spindle-shaped. Internal reproductive tract (Fig. 8A) with two-chambered bursa copulatrix (Fig. 8A:b), distal chamber cleft slightly, possibly forming spermatheca (Fig. 8A:s); slender, elongate spermathecal gland (Fig. 8A:g) attached by narrow duct to distal chamber (= spermatheca).

Natural History.—Little has been published on the biology or habits of species of *Ischyomius*. Champion (1916) stated that specimens of *I. chevrolati* were common in dead banana leaves in Panama. The information below was derived from the label data of specimens examined. Specimens of *I. chevrolati* were collected from wilted foliage of several species of Musaceae: *Musa sapientum* L. (banana), *M. paradisiaca* L. (plantain), and *M. textilis* Née. This species was found among banana debris at several quarantine interception points in the USA. Most of the individuals of *I. singularis* were collected by beating dry banana leaves on a plantation. Specimens of *I. nevermanni*, new species, were taken from foliage of two genera of Palmae: *Cryosophila* (= *Acanthorrhiza*) *warscewiczii* (H. Wendl.)

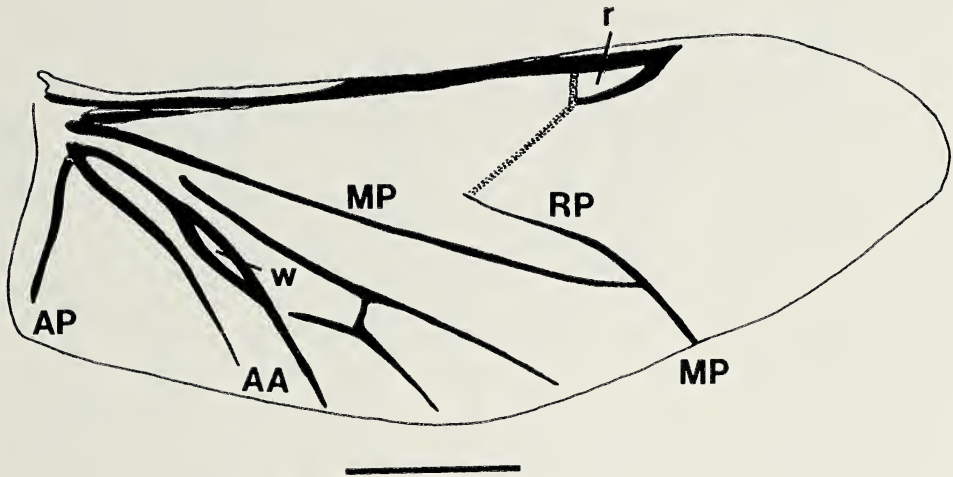


Fig. 5.—Flight wing of *I. singularis*. Scale bar = 2 mm.

Bartlett and *Iriarte* sp. A specimen of *Ischyomius bicolor* was collected in a fallen palm (*Orbigna phalerata* Martius) frond in Brazil.

Distribution.—The species of *Ischyomius* exhibit a Neotropical distribution, with a range that extends from Costa Rica, through Panama, into northwestern South America as far south as central Brazil (the latter based on one potentially dubious record).

KEY TO SPECIES OF *ISCHYOMIUS* CHEVROLAT

- 1. Pronotum with distinct bead along entire posterior margin (in most specimens); abdominal ventrites 1–4 with obvious vestiture 2
- 1'. Pronotum without posterior bead, or present laterally only; abdominal ventrites 1–4 without obvious vestiture 4
- 2 (1). Antennomeres filiform; elytral apex with conspicuous, outer spine (Fig. 1A–D, F) 3
- 2'. Antennomeres short, subserrate; elytral apex without conspicuous, outer spine (Fig. 1E) *Ischyomius bicolor* Champion
- 3 (2). Antennomeres 2–10 piceous to black, contrasting in color to antennomeres 1 and 11; lateral margins of pronotum with several long setae; body testaceous, with median, longitudinal dark vitta extended from frons to elytral apex (Fig. 1D) *Ischyomius championi*, n. sp.
- 3'. Antennomeres 1–11 concolorous, rufous; lateral margins of pronotum without long setae; body testaceous to rufous with elytral infuscation, around scutellum and rectangular to diamond-shaped, transverse dark area slightly posterior of elytral midlength (Fig. 1F) *Ischyomius nevermanni*, n. sp.
- 4 (1'). Anterolateral angles of pronotum produced, square to slightly acute (Fig. 1C) *Ischyomius denticollis* Champion
- 4'. Anterolateral angles of pronotum not produced, more or less rounded 5
- 5 (4'). Lateral margins of pronotal disc evenly arcuate (Fig. 4C); lateral pronotal bead not attaining anterior pronotal margin (Fig. 4D); lateral margins evenly convex to edge *Ischyomius chevrolati* Champion
- 5'. Lateral margins of pronotal disc straighter (Fig. 4A); lateral pronotal bead attaining anterior pronotal margin (Fig. 4B); lateral margins explanate, flat to slightly concave to lateral edge *Ischyomius singularis* Chevrolat

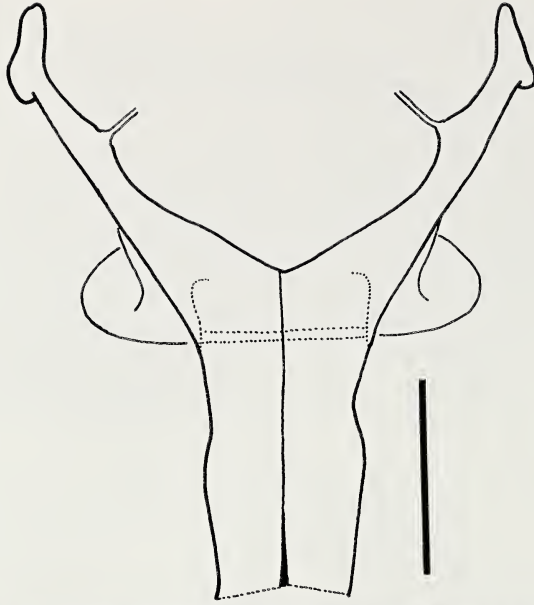


Fig. 6.—Metendosternite of *I. singularis*. Scale bar = 0.5 mm.

Ischyomius singularis Chevrolat

(Fig. 1A; 3A, D; 4A, B; 5; 6; 7D; 10)

Ischyomius singularis Chevrolat, 1878:98; Champion, 1916:81; Csiki, 1924:6; Blackwelder, 1945:494.

Type Specimens.—Lectotype, here designated, female, labelled: “[green label with illegible handwritten locality] / Muséum Paris 1906 Coll. L. FAIRMAIRE / [red label] TYPE / [handwritten] *Ischyomius singularis* Chev Bogota”, (MNHN, coll. Fairmaire). Paralectotype male, labelled: “[green label] N Grenad Honda Goudon / Muséum Paris 1906 Coll. L. FAIRMAIRE / [red label] TYPE” (MNHN, coll. Fairmaire).

Taxonomic Notes.—One specimen from OXUM bears the label “*Amphora complanata* de Brême.” This specimen was mentioned by Champion (1916) as having been given to the BMNH in 1871 as part of the Bowring Collection. Although the label on this specimen predates Chevrolat’s description, Champion states that *Amphora complanata* is a manuscript name only and he does not question the validity of *I. singularis*. *Amphora* is already twice pre-occupied in zoology, once for an echinoderm and once for a weevil (Neave, 1939). Another specimen in BMNH has the label “*Amphora* sec. Doué’s coll.” I have been unable to find a citation for *A. complanata*, and it is here discarded as an available name.

Diagnosis.—*Ischyomius singularis* is one of the three unicolorous species in the genus. Its diagnostic features include the mental pit in the male (Fig. 3A) and carinate lateral pronotal margin (Fig. 4A, B). *Ischyomius singularis* is structurally similar to *I. denticollis*, but lacks the produced anterolateral pronotal angles of the latter. Pronotal features separating *I. singularis* and *I. chevrolati* are given in the key.

Description.—TL 6.9–13.4; GEW 1.8–3.5. Color uniformly rufotestaceous to rufopiceous. Eyes relatively small, nonprotuberant; antennae relatively long, antennomeres 5–10 filiform, elongate; male

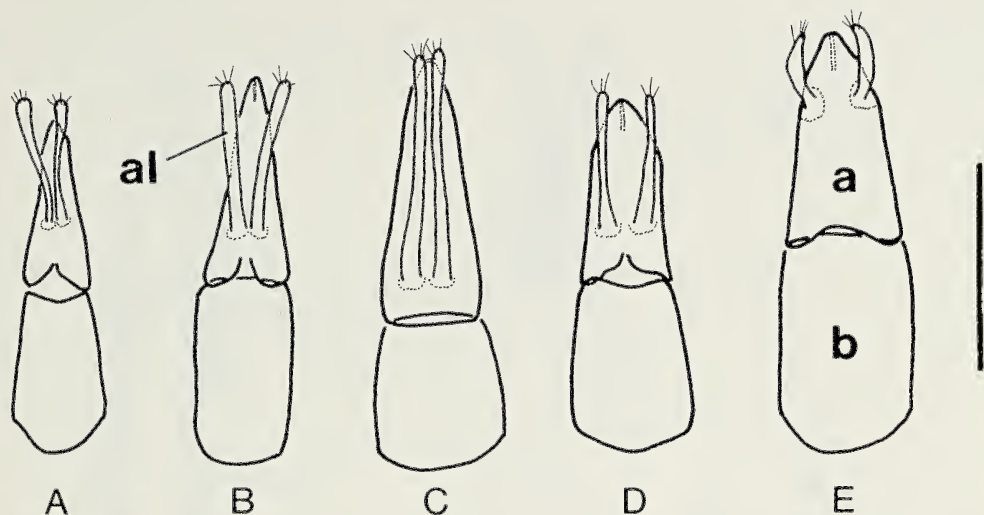


Fig. 7.—Aedeagi of *Ischyomius* spp., median lobe removed, dorsal. A, *I. bicolor*; B, *I. nevermanni*, n. sp.; C, *I. chevrolati*; D, *I. singularis*; E, *I. denticollis*. a = apicale, al = accessory lobe, b = basale. Scale bar = 0.5 mm (A–D), 0.8 mm (E).

with pit on mentum; dorsal punctation relatively coarse, sparse, shallow. Pronotum wider than long (GPW/PL 1.2–1.4), without elongate, erect setae; posterior bead absent; lateral margin of disc variously crenulate, or tuberculate, widest anterior of midlength; anterolateral angles rounded; disc relatively flat, slightly explanate to lateral margins, with distinct posterolateral depressions; lateral carina distinct, present to anterior margin; punctation relatively shallow, irregular. Elytra without regular, erect setae; apical spine very long; punctation fine, shallow. Tarsomeres (all but distal) greatly expanded. Venter of abdomen without distinct vestiture. Aedeagus relatively stout, with apicale subequal in length to basale; apicale broad, almost parallel-sided; accessory lobes relatively elongate, inserted proximad to apicale midlength.

Other Material Examined.—**BOLIVIA.** Country record only, (SMTD, 1). **COLOMBIA.** *Magdalena:* San Sebastian de Rabago, Sierra Nevada de Santa Marta, 2000 m, 11–14.iv.1968, B. Malkin, beating dry banana leaves on plantation, (FMNH, 43); same locality, except 12–13.iv.1968, ex dry banana leaves on banana plantation, (FMNH, 28). *Valle:* nr. Pichinde, 5000', 18.vii.1970, H. & A. Howden, (CNC, 1). Country records only, (OXUM, 1), (BMNH, 2). **ECUADOR.** *Bolivar:* Balzapamba, 1500 m, (MNHN, 3). *Chimborazo:* Chimbo [= Puente de Chimbo], M. de Mathan, 1891, (MNHN, 2). *Napo:* Lago Agrio (41 Kms. W.), 18.v.1975, Spangler et al., Ecuador–Peace Corps–Smithsonian Institution Aquatic Insect Survey, (NMNH, 1); Limoncocha, 250 m, 9–16.iii.1976, J. M. Campbell, (CNC, 2). *Pastaza:* Cusuimi, Rio Cusuimi, 150 km SE Puyo, 300 m, 15–31.v.1971, B. Malkin, (FMNH, 2); same data, except 300 m, 18–23.vii.1971, (FMNH, 1); 8 km NE Puyo, 28.iv.1978, C. W. & L. B. O'Brien & Marshall, (FSCA, 1). *Pichincha:* 47 km SE Sto. Domingo, Rio Palenque Sta., 300 m, 22–28.ii.1976, J. M. Campbell, (CNC, 1). **PERU.** *Huánuco:* Yurac, 67 mi E. of Tingo Maria, 11.xii.1954, E. I. Schlinger & E. S. Ross, (CASC, 1). *Lima:* Callanga, (FMNH, 8), (NMNH, 2). **General locality** (not mapped). Nova Grenada, (BMNH, 1).

Geographical Distribution.—All examined specimens of *I. singularis* were collected in northwestern South America (Fig. 10).

Ischyomius chevrolati Champion
(Fig. 1B; 2; 3B, C; 4C, D; 7C; 8; 11)

Ischyomius chevrolati Champion, 1916:82; Csiki, 1924:6; Blackwelder, 1945:494.

Type Specimens.—Lectotype, male, here designated, left specimen on card with two specimens, labelled: “V. de Chiriqui, 25–4000 ft. Champion. / [round label

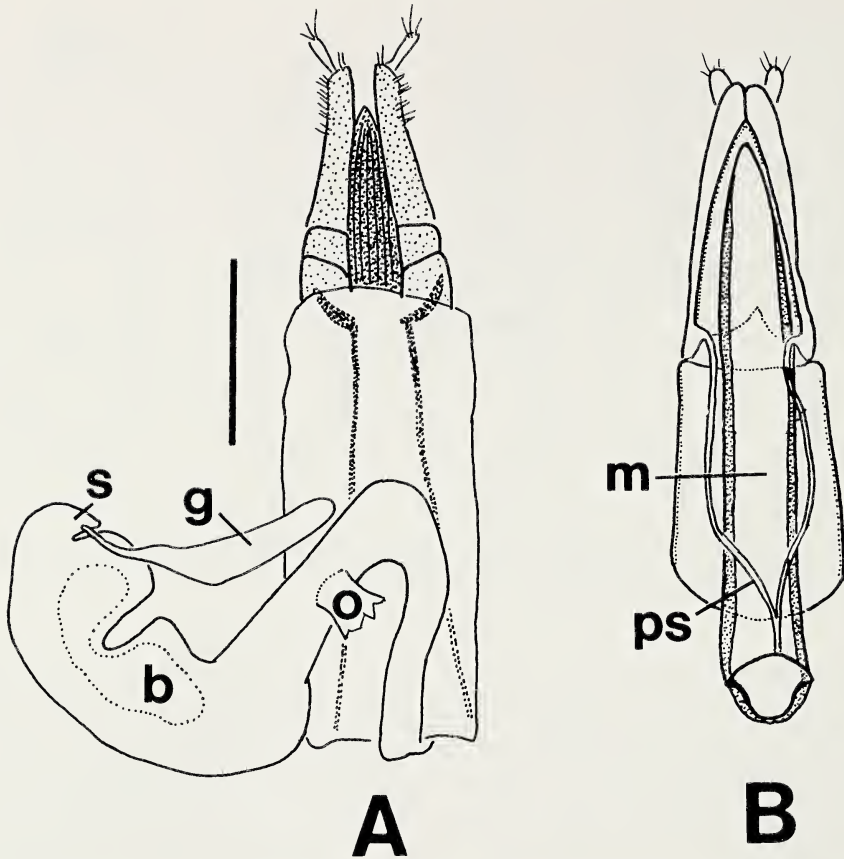


Fig. 8.—A, ovipositor and reproductive tract of female *I. chevrolati*; B, aedeagus of *I. chevrolati*, ventral. b = bursa copulatrix, g = spermathecal gland, m = median lobe, o = oviduct, ps = parameral strut, s = spermatheca. Scale bar = 0.5 mm.

with red margin] Type H. T. / [male and female biological symbols] / *Ischyomius chevrolati*, Ch / B.C.A. Col. IV. 2. *Ischyomius singularis* Chev. Champ. / [round label with blue margin] SYNTYPE" (BMNH). Paralectotype, female, mounted on same card as lectotype. Two paralectotypes, mounted on one card, one female, the other sex indeterminate, labelled: "V. de Chiriqui, 25–4000 ft. Champion. / B.C.A. Col. IV. 1. *Ischyomius singularis* Chev. Champ. / *Ischyomius singularis* Chev. / [round label with blue margin] SYNTYPE" (BMNH).

Ischyomius singularis Champion (not Chevrolat) 1886:259, pl. 11, fig. 17 and 17 a, b, c.

Diagnosis.—*Ischyomius chevrolati* is recognized by the following features: body unicolorous; males without mental pit; pronotum with lateral margin smooth, carina dorsal (Fig. 4C, D). Among the other unicolorous species of *Ischyomius*, *I. chevrolati* lacks the produced anterolateral pronotal angles of *I. denticollis* (Fig. 1C) and has a different pronotal structure than *I. singularis* (Fig. 4A, B).

Description.—TL 7.7–11.4; GEW 2.2–3.2. Color uniformly rufotestaceous. Eyes relatively small, nonprotuberant; antennae long, antennomeres filiform, relatively elongate; male without pit on mentum; punctation relatively coarse, more or less uniformly spaced. Pronotum wider than long (GPW/

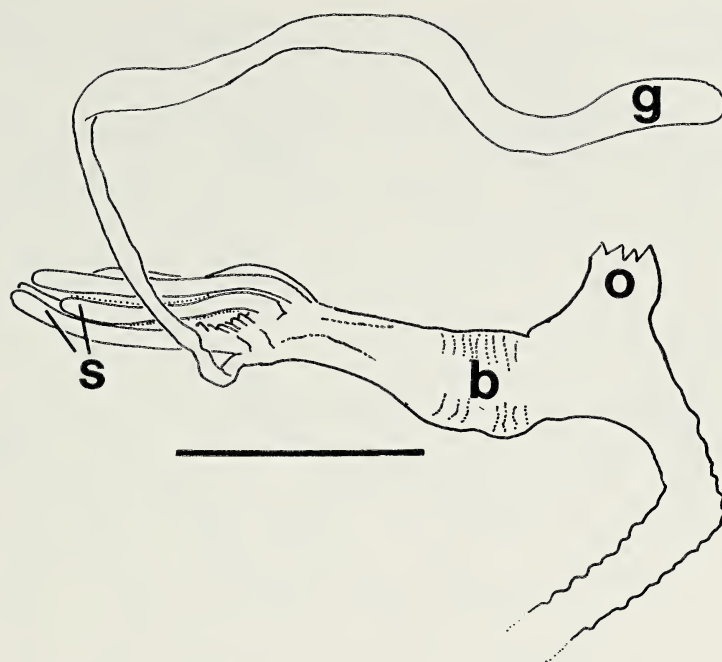


Fig. 9.—Reproductive tract of female *Trictenotoma* sp. b = bursa copulatrix, g = spermathecal gland, o = oviduct, s = spermatheca(e). Scale bar = 1 mm.

PL 1.3–1.4), without elongate, erect setae; posterior pronotal bead absent; lateral margin of disc smooth, parallel-sided basally, and evenly arcuate to anterior margin; anterolateral angle rounded; disc relatively convex, not explanate laterally, with slightly developed posterolateral depressions; lateral carina indistinct, not present to anterior margin; punctation relatively shallow. Elytra without regular, erect setae; apical spine moderately long; punctation deep and coarse. Tarsomeres (all but distal) moderately expanded. Venter of abdomen without distinct vestiture. Aedeagus relatively slender, with basale distinctly shorter than apicale; apicale evenly tapered apically; accessory lobes very long and slender, inserted toward base of apicale.

Other Material Examined.—**COSTA RICA.** *Cartago–Limón border:* 40 km NE Turrialba, 500 m, 18.v.1979, H. & A. Howden, (CNC, 1). *Limón:* Valle de la Estrella, Valle de Rosas, nr. Pandora, 17.ii.1984, H. & A. Howden, (DAPC, 1); Finca Hamburgo, F. Nevermann, (MUCR, 1); Hamburg Farm, Reventazon Ebene, Limon, 26.x.1934, F. Nevermann, welkem Blatt von *Musa sapientum*, (NMNH, 1); same data, except 28.xii.1934, (NMNH, 3); same data, except 20.ix.1935; same data, except 3.xi.1927, (NMNH, 3); same locality, 25.x.1934, welkem Blatt von *Musa paradisiaca*, (NMNH, 1); same locality, 6.ii.1928, an welkem Bananenblatt, (NMNH, 1); same locality, 30.vii.1934, an welkem Laub *Musa textilis*, (NMNH, 1); same locality, 20.ix.1935, welkem Blatt von *Musa sapientum*, (NMNH); Las Mercedes, Sta. Clara, 200–300 m, 6.viii.1922, F. Nevermann, (NMNH, 1); Guapiles, Sta. Clara, 250–300 m, 22.iv.1935, welkem Blatt von *Musa sapientum*, F. Nevermann, (NMNH, 1); Las Mercedes, 12.vii.1922, F. Nevermann, (NMNH, 1). *Puntarenas:* Osa Peninsula, habitat near Sirena, 0–5 m, xi.1983, S. H. Boinski, (CMNH, 1); same locality and collector, v.1984, coll. on living foliage in second growth forest, (CMNH, 2); same locality and collector, xi.1983, coll. on dead foliage, (CMNH, 2; DAPC, 1); viii.1984, second. forest with bamboo, coll. on dead foliage, (CMNH, 2; DAPC, 1); viii.1984, coll. on dead foliage in second growth forest, (CMNH, 1); vi.1984, ex. sweep sample in second growth forest, (CMNH, 1); vi.1984, coll. on dead foliage in secondary growth forest, (CMNH, 1; DAPC, 1); Monteverde, 1400 m, 23.v.1979, H. & A. Howden, (CNC, 4); same locality, 21.viii.1987, H. & A. Howden, (DAPC, 1). *San José:* Coronado, 1400–1500 m, 15.viii.1931, F. Nevermann, welkem Blatt von *Musa sapientum*, (NMNH, 1); San José, 1000–1100 m, 26.viii.1928, F. Nevermann, (NMNH, 2); San Jose, 19.vi.1962, L. Berkeley, woodland farmland window, night, (FSCA, 1). *Quarantine records:* on banana debris, ex Costa Rica, N.Y. 46434, (NMNH, 2); on banana

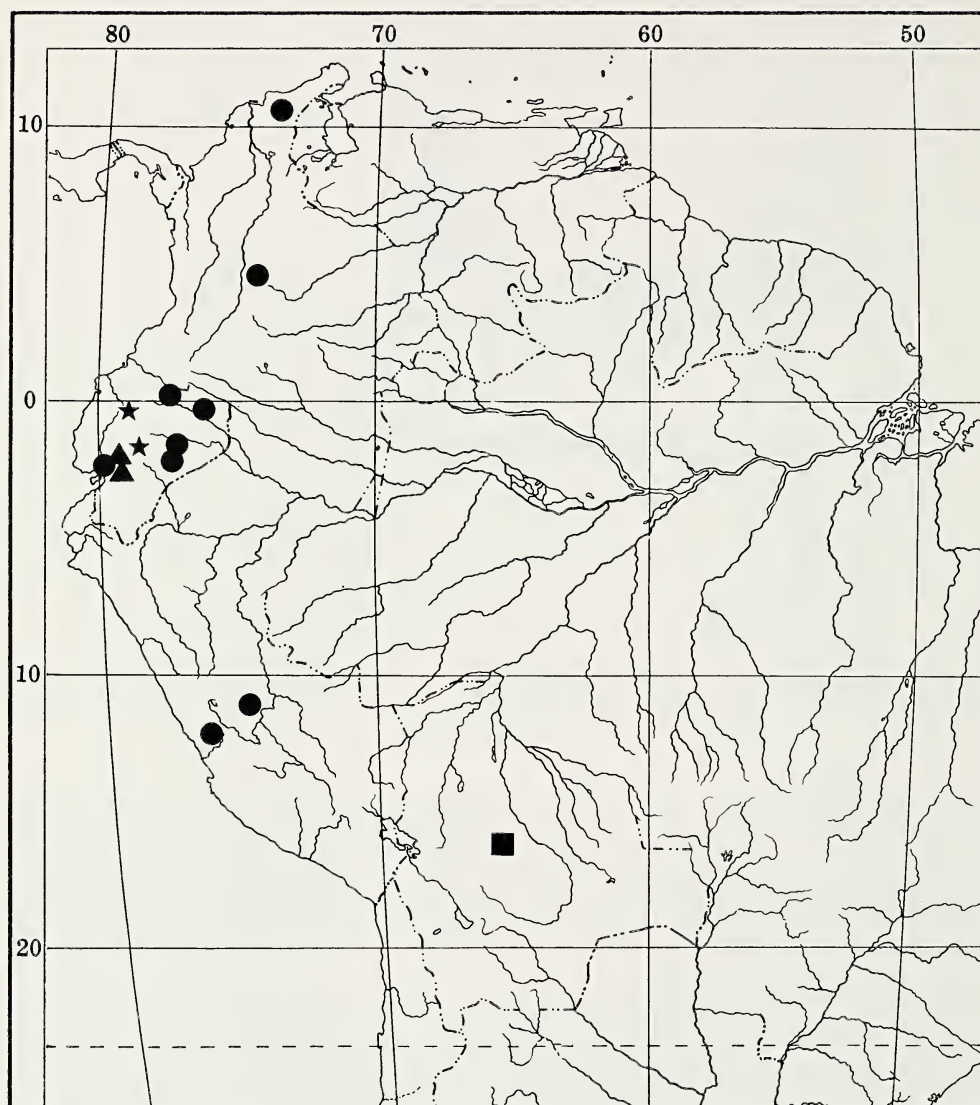


Fig. 10.—Known distribution of *I. singularis* (dots and stars) and *I. denticollis* (triangles and stars). Square represents country record (Bolivia) for *I. singularis*.

trash, ex Costa Rica, N.Y. No. 23993, (NMNH, 1); on banana ex Costa Rica 8.vii.1935, N.Y. 44942, (NMNH, 1). *Locality not found or mapped*: San Vito, 25.v.1983, (AAAC, 1). **PANAMA**. *Canal Zone*: Frijoles, on Musaceae, E. A. Schwarz, (NMNH, 1). *Chiriquí*: 2 km N. Sta. Clara, 1300 m, Hartmann's Finca 8°51'N 82°46'W, 20.v.1977, H. & A. Howden, (CNC, 4); Hartmann's Finca, 19.v.1996, R. Turnbow, (RHTC, 2); V. de Chiriquí, 25–4000 ft., Champion, (NMNH, 4); 27.7 km W. Volcan Hartmann's Finca 08°45'N, 82°48'W, 1450 m, 14–17.vi.1995, J. Ashe & R. Brooks, ex slash, (SEMC, 1); Fortuna Dam, 16.v.1992, E. Giesbert, (FSCA, 1). *Quarantine records*: on banana debris ex Panama, 14.i.1937, Mobile 5581, (NMNH, 1); ex Panama Mobile Al 29.i.1934, in debris of banana Mob. # 1852, S. S. Sheffield, (NMNH, 1); Panama, 24.iv.1931, B. Bryant, on banana S. E. # 2585, (NMNH, 3). **VENEZUELA**. *State unknown*: Los Camales [= Canales?], G. Vivas B., (FMNH, 1).



Fig. 11.—Known distribution of *I. chevrolati*.

Geographical Distribution.—All but a single examined specimen of *I. chevrolati* were collected in Costa Rica and Panama (Fig. 11). A single record is known from northern Venezuela, based on a questionable locality. “Los Camales” has here been interpreted as a misspelling of “Canales,” and mapped accordingly.

Ischyomius bicolor Champion
(Fig. 1E; 7A; 12)

Ischyomius bicolor Champion, 1916:82; Csiki, 1924:6; Blackwelder, 1945:494.

Type Specimen.—Holotype, sex unknown, labelled: “Sarayacu, Ecuador. C. Buckley. / [label with horizontal green line through middle] Sarayacu 80.14 / [round label with red margin] Type H. T. / *Ischyomius bicolor*, Ch” (BMNH).

Pseudoischyomius rufipennis Pic, 1923:21; Blackwelder, 1945:494.

Type Specimen.—Holotype, sex unknown, labelled: “Iguapo / [yellow label] type / [red label] TYPE / Museum Paris coll. M. Pic / *Pseudoischyomius* n gen rufipennis n sp”, (MNHN). New synonymy.

Taxonomic Notes.—Two forms of *I. bicolor* were examined in this study. All but one of the specimens agreed very closely with the types of both *I. bicolor* and *Pseudoischyomius rufipennis*. One specimen, however, is considerably shorter and exhibits characters not found in the other specimens. Notably, the lateral margins of the pronotal disc have several crenulations in the anterior half and the body color is atypical (see diagnosis below). I judged this individual to be an aberrant specimen of *I. bicolor*, although discovery of additional material may necessitate a closer examination of its status.

Diagnosis.—*Ischyomius bicolor* is the only species in the genus with relatively short, serrated antennae, and lacking the apical elytral spine. Also, in all but one specimen, the pronotal color is dark and contrasts that of the elytra. In the one

aberrant specimen the pronotum and elytra are concolorous, the latter with an infusate area along the suture.

Description.—TL 7.9–12.1; GEW 2.3–3.4. Color of two forms; typical: head and pronotum piceous, elytra rufous; atypical: body rufous with area along elytral suture infuscated, not extended to apex. Eyes large, protuberant; antennae relatively short, antennomeres 5–10 moniliform/subserrated; males without pit on mentum; punctuation fine, relatively sparse. Pronotum distinctly wider than long (GPW/PL 1.4–1.5), with few long marginal setae; posterior pronotal bead distinct; lateral margins of disc subparallel-sided basally, arcuate anteriorly; lateral margin with several crenulations in anterior half in one specimen (see taxonomic notes); anterolateral angle rounded; disc slightly convex, not explanate; lateral carina distinct, present to anterior margin; punctuation relatively shallow. Elytra with several rows of erect setae, especially toward lateral margin; apical spine very short, indistinct. Tarsomeres moderately expanded. Venter of abdomen with distinct vestiture. Aedeagus slender, with apicale very slightly longer than basale; apicale slender, evenly tapered apically; accessory lobes slender, enlarged apically, inserted slightly proximal of midlength of apicale.

Other Material Examined.—**BRAZIL**. *Amazonas*: São Paulo de Olivença, M. de Mathan, (MNHN, 1). *Rondônia*: 62 km. SW Ariquemes, Fzda. Rancho Grande, 11.xi.1994, C. W. & L. B. O'Brien, in fallen frond babaçu palm, Orbigna phalerata Martius, (DAPC, 1). **COLOMBIA**. *Amazonas*: Leticia, 700', 10.vii.1970, H. & A. Howden, (CNC, 4). **ECUADOR**. *Pastaza*: Cusuimi, Rio Cusuimi, 150 km SE of Puyo, 15–31.v.1971, B. Malkin, (FMNH, 1). **PERU**. *Loreto*: Iquitos, M. de Mathan, (MNHN, 2). *Madre de Dios*: Tambopata Wildlife Res, 30 km SW Pto. Maldonado, 12°50'S, 69°20'W; 290 m, 9.xi.1982, J. J. Anderson, (CMNH, 1).

Geographical Distribution.—*Ischyomius bicolor* is found in NW South America, and its aggregate range extends further east and south than the other South American species of the genus (Fig. 12). The type specimen of *Pseudoischyomius rufipennis* was collected in "Iguapo." A search of atlases and gazetteers failed to locate such a locality. However, there are four separate populated places in Brazil called "Iguape" (two in Bahia and one each in Espírito Santo and São Paulo), one of which might represent the type locality of *P. rufipennis*.

Ischyomius denticollis Champion (Fig. 1C; 10)

Ischyomius denticollis Champion, 1916:81; Csiki, 1924:6; Blackwelder, 1945:494.

Type Specimen.—Holotype, male, labelled: "44 / [green label] 160 / [round label with red margin] Type H. T. / [label upside down] 71.6 / [handwritten, partly illegible label, something like "pres du uloma"] / *Ischyomius denticollis*, Ch" (BMNH).

Diagnosis.—*Ischyomius denticollis* is recognized easily by the produced anterolateral pronotal angles (Fig. 1C). Males of *I. denticollis* possess the large mental pit found also in *I. singularis*. The structure of the aedeagus (Fig. 7E) of *I. denticollis* is unique in *Ischyomius*: the accessory lobes are very short, curved, and inserted toward the distal end of the apicale.

Description.—TL 10.6–12.3; GEW 2.7–3.2. Color uniformly rufotestaceous. Eyes large, protuberant; antennae moderately long, antennomeres 5–10 filiform, relatively elongate; male with pit on mentum; punctuation fine, sparse, shallow. Pronotum distinctly wider than long (GPW/PL 1.3–1.4), without elongate, erect setae; posterior pronotal bead absent; lateral margin of disc smooth, widest at anterolateral angle; anterolateral angle produced, acute; disc convex, not explanate laterally, with slightly developed posterolateral depressions; lateral carina distinct, present to anterior margin; punctuation relatively shallow, more or less regularly spaced. Elytra without regular, erect setae; apical spine very long; punctuation moderately coarse. Tarsomeres (all but distal) moderately expanded. Venter of abdomen without distinct vestiture. Aedeagus stout, apicale and basale subequal in length; lateral margins of apicale slightly convergent apically; accessory lobes short, curved, inserted near distal end of apicale.

Other Material Examined.—**ECUADOR**. *Bolívar*: Balzapamba, iii–iv.1894, M. de Mathan,

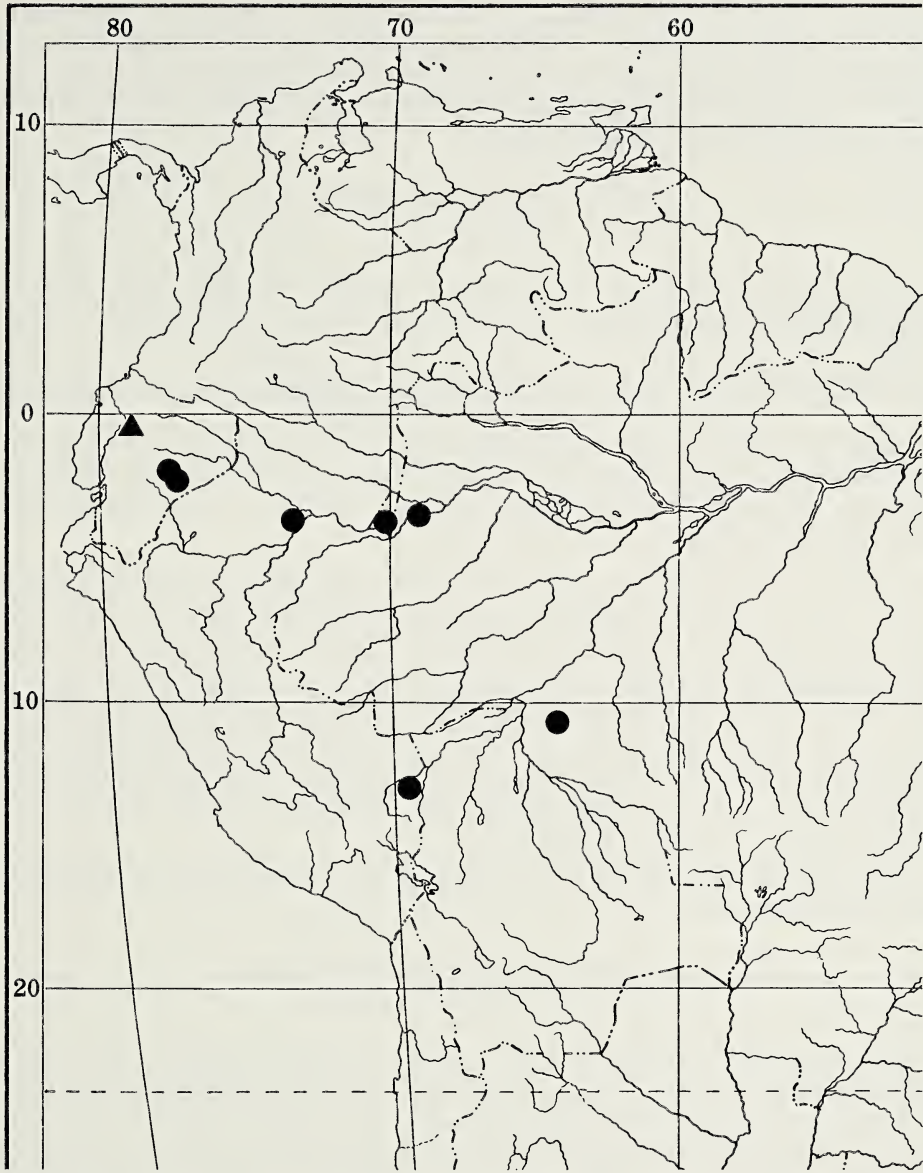


Fig. 12.—Known distribution of *I. bicolor* (dots) and *I. championi*, n. sp. (triangle).

(MNHN, 5); Balzapamba, Route de Quito, vii–viii.1893, M. de Mathan, (MNHN, 1). *Esmeraldas*: Cachabé [= Cachavi], xi.1896, Rosenberg, (MNHN, 1); same data except xii.1896, (MNHN, 1); Cachabé to Paramba [Imbadura Prov.], ii.1897, Rosenberg, (MNHN, 2). *Los Ríos*: Pichilingue, 40 m, 2.ii.1955, E. I. Schlinger & E. S. Ross, (CASC, 1). *Pichincha*: Rio Palenque, 47 km S. St. Domingo, 700', 22.ii.1976, H. & A. Howden, (CNC, 1). **Country unknown**: Manizales, A. M. Patino, (MNHN, 1).

Geographical Distribution.—All examined specimens of *I. denticollis* with reliable label data were collected in Ecuador (Fig. 10). Champion (1916) tentatively gives the locality of the type of *I. denticollis* as Colombia, although there is no

indication of this on the specimen. This specimen was obtained by BMNH in 1871 along with specimens of *I. singularis*, which were collected in Colombia (Champion 1916). This record is not included on Figure 10. A specimen from MNHN was collected at Manizales; since there is a Manizales in both Colombia and Ecuador, this record is not mapped.

Ischyomius championi, new species
(Fig. 1D; 12)

Type Specimen.—Holotype, sex unknown, labelled: "Ecuador, Pich. 47 Km SE Sto Domingo Rio Palenque Sta. II.22–28.1976 300 m J. M. Campbell" (CNC).

Derivation of Specific Epithet.—This species is named in honor of George C. Champion (1851–1927), who was a pioneer in the systematics of *Ischyomius* and many other groups of Tenebrionoidea.

Diagnosis.—Among *Ischyomius*, this species is unique in having the body color testaceous with a central dark vitta extending from the head to near elytral apex (Fig. 1D). The only other constantly maculate species, *I. nevermanni*, has the contrasting color pattern on the elytra only.

Description.—TL 9.5; GEW 2.2. Color testaceous with antennomeres 2–10 piceous; antennomere 11 rufous; dorsum with narrow, longitudinal black vitta starting between eyes and extended to elytral apex, along suture. Eyes large, protuberant; antennae long, antennomeres 5–10 short, submoniliform; male with or without pit on mentum (single specimen examined of undetermined sex); punctuation coarse, irregularly spaced. Pronotum relatively elongate (GPW/PL 1.1), with several elongate, marginal setae; posterior pronotal bead distinct; lateral margins of disc subparallel-sided with few fine crenulations on each side; anterolateral angle rounded; disc moderately convex, not explanate laterally, with indistinct posterolateral depressions; lateral carina distinct, curved dorsally before attaining anterior margin; punctuation deep, coarse, relatively uniformly spaced. Elytra with rows of regular, erect setae, especially on lateral areas; apical spine relatively short. Tarsomeres moderately expanded. Venter of abdomen with distinct vestiture. Aedeagus not studied.

Geographical Distribution.—The holotype of *I. championi* was collected in western Ecuador (Fig. 12).

Ischyomius nevermanni, new species
(Fig. 1F; 7B; 13)

Type Specimens.—Holotype, male, labelled: "[green label] COSTA RICA F NEVERMANN 15.XI.26 / [green label, inverted] HAMBURGFARM REVENTAZON EBENE LIMON / [illegible handwritten label]" (NMNH). [Specimen dissected with abdomen mounted on card and genitalia in microvial beneath specimen]. Allotype, female, labelled: "[green label] COSTA RICA F NEVERMANN 25 X 35 / [green label, inverted] HAMBURGFARM REVENTAZON EBENE LIMON / an welkem Laub [with handwritten name]" (NMNH). Thirty-eight paratypes, sexes not determined. Twenty-six from same locality as holotype (DAPC, 1; CMNH, 1; FMNH, 2; NMNH, 22). Other paratypes as follows: **COSTA RICA**. *Cartago*: Turrialba, 650 m, 25.ii.1980, H & A Howden, (CNC, 1). *Guanacaste*: 2 mi. N. Bijagua, 13.ix.1990, 430 m, B. C. Ratcliffe, (DAPC, 1). *Heredia*: La-Selva, nr. Pto. Viejo 50 m 19.Feb.1980, H & A Howden, (CNC, 2). *Limón*: Guápiles, 6.x.1915, F. Nevermann, (NMNH, 4); Bananito, 20.iv.1925, F. Nevermann, (MUCR, 1); Escosia, 12.vi.1928, F. Nevermann, (MUCR, 2); Est. Cuatro Esquinas, 0 m, P. N. Tortuguero, xii.1992, R. Delgado, (INBC, 2). **PANAMA**.



Fig. 13.—Known distribution of *I. nevermanni*, n. sp.

PortoBello [= Portobelo], 28.ii.1911, E A Schwarz, (NMNH, 1). Panama: Parque Nacional Soberania, 23.v.1996, R. Turnbow, (RHTC, 2).

Derivation of Specific Epithet.—This species is named in honor of cucujid specialist Wilhelm Heinrich Ferdinand Nevermann, who collected most of the type material.

Diagnosis.—*Ischyomius nevermanni* is recognized easily by its maculate color pattern, expanded laterally on the elytra only (Fig. 1D). The only other species of *Ischyomius* with a distinct elytral macula is *I. championi*, in which the macula is linear and unexpanded laterally, and extends from the head to the elytral apex.

Description.—TL 5.9–10.5; GEW 1.5–2.8. Color testaceous to rufous; elytra with triangular, median infuscation along suture, expanded into transverse fascia, reaching or closely approaching lateral margins. Eyes very large, distinctly protuberant; antennae long, antennomeres 5–10 filiform, relatively short; male without pit on mentum; punctation relatively fine, sparse. Pronotum moderately elongate (GPW/PL 1.1–1.2), without distinct, marginal setae; posterior pronotal bead distinct, slightly indistinct medially in a few specimens; lateral margins of disc relatively straight, evenly divergent anteriorly, with or without shallow sinuations; anterolateral angle rounded; disc moderately convex, not explanate laterally, with indistinct posterolateral depressions; lateral carina distinct, not present to anterior margin; punctation moderately coarse, evenly spaced. Elytra with few scattered erect setae; apical spine relatively short. Tarsomeres only slightly expanded. Venter of abdomen with distinct vestiture. Aedeagus relatively slender, apicale slightly longer than basale; apicale evenly tapered to apex; accessory lobes slender, inserted basally on apicale.

Geographical Distribution.—*Ischyomius nevermanni* is known only from Costa Rica and Panama (Fig. 13). The record from Guanacaste Province represents the most northern record for the genus.

SYSTEMATIC PLACEMENT OF *ISCHYMIUS*

Familial Affinities

Analytical Approach.—Evidence is presented here to support the placement of *Ischyomius* within Pythidae, rather than Trictenotomidae, as suggested by Watt

(1987). The presence of parameral struts (Fig. 8B:ps) on the male genitalia places *Ischyomius* within the unresolved (Pythidae + Salpingidae + Trictenotomidae) clade of the salpingid group of families (Pollock, 1994). The following adult structural features define further the placement of *Ischyomius*.

Pit on Male Mentum.—Males of all Pythinae, except *Anaplopus* Blackburn, possess a small, circular to elliptical deep pit(s) of unknown function, through which often protrude a number of stiff setae or microtrichia (e.g., Pollock, 1991: fig. 5C, D; Young, 1976: fig. 9–11). Males of at least *I. denticollis* and *I. singularis* (Fig. 3A:p) have a similar pit. This feature is unknown in other examined members of the salpingid group, and, although not present in all species of *Ischyomius*, it still may be a synapomorphy for *Pytho* Latreille, *Priognathus* LeConte, *Sphalma* Horn, and *Ischyomius*. The pit is presumed lost in *Anaplopus* Blackburn and the remaining four species of *Ischyomius* (condition unknown in *I. championi*, n. sp.).

Structure of Internal Female Reproductive Tract.—Pollock (1994) stated that the presence of a double-chambered bursa copulatrix is a synapomorphy uniting genera of Pythidae. Pollock and Lawrence (1995) stated that all species they examined representing the genera of Pythidae possess the double-chambered bursa copulatrix. This was in error, because the bursa copulatrix in females of *Sphalma* is actually single-chambered. This may represent a reversal of the apomorphic state present in all other genera of Pythidae. The bursa copulatrix in *Ischyomius* is double-chambered (Fig. 8A:b), while in *Trictenotoma* Blanchard it is elongate and single chambered (Fig. 9:b).

Arrangement of spermathecae and accessory glands was shown to be important in classifying constituents of the salpingid group (Watt, 1987; Pollock, 1994, 1995). Two different types of spermathecae are found in Pythidae. In one type, including *Ischyomius* and *Sphalma*, the spermatheca is formed by a narrowing of the distal chamber of the bursa copulatrix (Fig. 8A:sp). The spermatheca in *Pytho* and *Priognathus* is undifferentiated. In *Trictenotoma*, the spermatheca is divided into six relatively short, elongate branches, in three groups of two (Fig. 9:sp).

In most species of Pythidae, an accessory gland is present, joined to one of the two chambers of the bursa copulatrix (e.g., Pollock and Lawrence, 1995: fig. 17). This gland is absent from representatives of two species groups of *Pytho*, however. Females of *Ischyomius* have an elongate accessory gland (Fig. 8A:g). Females of *Trictenotoma* have a very long elongate accessory gland (Fig. 9:g) attached to the distal end of the bursa copulatrix.

Additional research is needed to resolve fully the homologies among the various structures of the internal female reproductive tract within the Tenebrionoidea, and specifically, the salpingid group. However, the presence of the double-chambered bursa copulatrix and the structure of the accessory gland suggest an affinity of *Ischyomius* with Pythidae.

Structure of Male Genitalia.—An analysis of male genitalia similarly indicates an affinity of *Ischyomius* with Pythidae, rather than Trictenotomidae. Taxa of both families exhibit basic structural similarities of the male genitalia and were thought to be closely related by Pollock (1994). The two main parts of the tegmen, the basale and apicale (Fig. 7E:b and a), are of more or less equal length in pythids. In trictenotomids the basale is very short, and the apicale is about four times the length of the basale (Sharp and Muir, 1912). In *Ischyomius*, the paired accessory lobes (Fig. 7B:a) articulated to the apicale are relatively short, and are with few, short apical setae. In males of Trictenotomidae, the accessory lobes are very long, with long, dense, apical setae (Sharp and Muir, 1912). Within the salpingid group,

the presence of parameral struts (as opposed to basal struts) on the aedeagus was thought to be a synapomorphy of (Trictenotomidae + Salpingidae + Pythidae) by Pollock (1994). Males of *Ischyomius* have distinct parameral struts (Fig. 8B: ps) that are membranous towards the base of the median lobe, and a basally cylindrical aedeagus characteristic of other Pythidae.

Structural Differences Between Ischyomius and Other Pythidae.—In addition to the above similarities between *Ischyomius* and other Pythidae, there are certain important differences, including the size and shape of the procoxal process and the shape of the tarsomeres. All other taxa of Pythidae have a relatively short procoxal process, not extended posterad of the coxae (e.g., see Pollock, 1991:fig. 7A, B). The procoxal process in *Ischyomius* is larger, expanded posteriorly, and extends behind the procoxae (Fig. 3C). Adults of *Pytho*, *Priognathus*, *Sphalma*, and *Anaplopus* have simple, unexpanded tarsomeres, while those of *Ischyomius* are distinctly widened (Fig. 3D).

Conclusion.—Although admittedly aberrant, *Ischyomius* should be retained in Pythidae and not in Trictenotomidae as suggested by Watt (1987). Discovery and description of the larva of *Ischyomius* will be extremely important in either corroborating or refuting this family placement.

Position of Ischyomius Within Pythidae

Pollock and Lawrence (1995) discussed the constituents of Pythidae and some of the more important characters defining the genera. However, they did not provide a detailed phylogenetic analysis of the characters. In spite of this, some speculative comments regarding the placement of *Ischyomius* within Pythidae are presented here.

Among other genera of Pythidae, *Ischyomius* shares several features with *Sphalma*. In both genera, the antennal insertions are concealed dorsally (Pollock and Lawrence, 1995); this feature is most distinct in *Sphalma*. In species of both genera, the mandibular mola is very large (Fig. 2C:m; 3B; Pollock, 1995:fig. 25), with the prostheca (Fig. 2F:p) proximal and distal to it (this type of mola is found also in *Anaplopus* [Pollock and Lawrence, 1995:fig. 10]). Also, dorsally on the mandibular base, there is a notch just lateral of the mola (Fig. 2A, D:n), that among pythids is found only in *Ischyomius* and *Sphalma*. The lateral pronotal carinae in *Ischyomius* and *Sphalma* are distinct, and visible dorsally for their entire lengths. The pronotum in *Pytho*, *Priognathus*, and *Anaplopus* is smooth, without lateral carinae.

From this and other studies on genera of Pythidae, the following three groups (these are not yet proven to be monophyletic) are postulated: 1) *Sphalma* and *Ischyomius*, 2) *Pytho* and *Priognathus*, and 3) *Anaplopus*. According to Pollock and Lawrence (1995), the genera *Osphyoplesius* Winkler and *Trimitomerus* Horn should be placed also in Pythidae; discovery and/or description of the larvae of these two genera will strengthen or refute their placement. The phylogenetic relationships among these genera will form the subject of subsequent research in this family.

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REVIEW

MAPLES OF THE WORLD. D. M. van Geldersen, P. C. de Jong, and H. J. Oterdoom. 1994. Timber Press, Inc., Portland, Oregon. 512 pp. ISBN 0-88192-000-2 (cloth). \$65.00.

Maples of the World, a monumental achievement and decades in preparation, is the first major world-wide monograph of the genus *Acer*. Maples are among the largest and most significant of woody plant groups in the Northern Hemisphere, with 124 species throughout the temperate zones. The dominant and colorful role of maples in the temperate deciduous forest, as well as their ornamental and economic uses, are only matched in importance by their taxonomic complexity.

The volume's first six chapters provide background information relating to the propagation, diseases and pests, structure, paleobotany and evolution, and finally, classification of maples. These are good chapters, but occasionally generalizations creep in where the authors try to summarize information about such a large and geographically diverse group. For example, the Aceraceae is circumscribed in a narrow, traditional, temperate-based sense with two genera—*Dipteronia* (two species in central China) and *Acer*—and not viewed more globally as relatives of a larger, tropical assemblage, the Sapindaceae. The traditional view of the family, however, will be familiar to those in the Northern Hemisphere.

The review of past classification schemes of maples and their weaknesses is meticulous, but soulfully lacks contemporary studies using molecular technologies, especially nucleic acids. However, when major molecular works with maples are done, they must be checked against some morphological monograph in which names and types have been accounted for. It will be this volume that will be the standard base-line reference. The authors do present an updated, phylogenetic system of classification based in large part on the previous work of Pojárkova (1933), de Jong (1976), and Delendick (1981). The volume's taxonomic synopsis of the family will be the beginning point for future maple systematic work.

The bulk of the text is devoted to species accounts, followed by the hybrids and cultivars. The 124 species, 95 subspecies, eight varieties, and a single form are divided by the authors into 15 sections with eight of these sections further subdivided into 19 series. Fourteen new combinations, 12 at the subspecific rank, one at the varietal rank, and one new section, are proposed. The detailed species descriptions are remarkably parallel, each with an extensive account of synonyms. Seven appendices contain relevant information that adds to the work's focus. No fewer than 35, double-column pages are required to list the cultivar names of the Japanese *Acer palmatum*, "akai washino o" to "yushide." Four cultivars are listed for *Acer pensylvanicum*, our native, eastern "moosewood" or "striped maple."

The exhaustive bibliography covering nearly 70 pages is one of most encyclopedic that I have seen. Contrasting with this inclusive documentation is the almost artistic presentation of maple diversity, much in color; all those gems of morphological variation unfold like variations on a Mozart concerto.

One familiar with the palmate leaves of "sugar maple" (*Acer saccharum*) is in for a fantastic surprise as one finds various simple and compound-leaved ma-

ples. These examples reveal our eastern North American "box-elder" or "ash-leaved maple" (*Acer negundo*) to be just another member of the family. In Southeast Asia, there are also evergreen (nondeciduous) maples—*Acer coriaceifolium* (China), *A. laevigatum* (China, Nepal), and *A. laurinum* (China, Malaysia to Philippines).

For students of vicariant plant geography, the book describes the Asian maples, all with parallel patterns of evolution and disjunction, on the opposite side of the world. Ecologically, plant-hardiness zones are cited for each species and cultivar. However, maps of plant-hardiness zones are only given for North America and Europe; none are presented for eastern Asia, which is a bit disconcerting since so many maple species and cultivars are east Asian in origin.

Timber Press should be commended on their devotion to high binding standards and editorial selection, neither of which have been neglected in this volume. This handsome volume will serve as the standard reference for students, specialists, and fanciers of maples for the next several decades, and perhaps longer. Its wide-ranging information is equally rewarding to scientists, landscape architects and designers, horticulturists, serious home gardeners, and all others with a genuine interest in trees. This book should be in every public library as well as on the shelf of anyone interested in temperate woody plants.

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CONTRIBUTION TO THE KNOWLEDGE OF THE
BRENTIDAE (INSECTA: COLEOPTERA) FROM TROPICAL AFRICA,
WITH REDESCRIPTION OF *PLESIOBOLBUS SAGAX* KOLBE

ALESSANDRA SFORZI¹

ABSTRACT

The author lists distributional data for 42 species of Brentidae from tropical Africa. Reported for the first time are distributional records from Senegal (1 sp.), Gambia (3 spp.), Mali (1 sp.), Republic of Guinea (8 spp.), Sierra Leone (2 spp.), Burkina Faso (1 sp.), Togo (2 spp.), Benin (1 sp.), Cameroon (15 spp.), Equatorial Guinea (2 spp.), Gabon (7 spp.), Angola (1 sp.), Zambia (1 sp.), Rwanda (5 spp.), Kenya (1 sp.), and South Africa (2 spp.). Remarks are given upon the geographic distribution of each species. The redescription of *Plesiobolbus sagax* Kolbe is also given.

KEY WORDS: Brentidae, tropical Africa, new records, *Plesiobolbus*

INTRODUCTION

Undetermined Brentidae (Insecta: Coleoptera) from the Ethiopian Region were studied in the entomological collections of the Carnegie Museum of Natural History (Pittsburgh, Pennsylvania, USA); additional data were added from other public and private collections (Muséum National d'Histoire Naturelle, Paris, France; Museum of Zoology and Entomology, Lund, Sweden; Zoologisk Museum, Copenhagen, Denmark; Prof. G. Osella, L'Aquila and Dr. L. Bartolozzi, Firenze, Italy; Mr. B. J. van Vondel, Hendrik Ido Ambacht, Holland). The following paper lists 42 species and includes many new records for the fauna of various tropical African countries. A specimen of *Plesiobolbus sagax* Kolbe was discovered, a species whose existence was seriously questioned by Damoiseau in his monograph on African Brentidae (1967a).

The following list follows the classification of tribes from Zimmermann (1994) and the species order of Damoiseau (1967a), awaiting a revised organization of the Brentidae which is urgently needed. Only papers published after Damoiseau's monograph, or not included in that work, are cited for each species.

INSTITUTIONAL ABBREVIATIONS

CBJV, collection of Mr. B. J. van Vondel, Hendrik Ido Ambacht, Holland; CGO, collection of Prof. Giuseppe Osella, L'Aquila, Italy; CLB, collection of Dr. Luca Bartolozzi, Firenze, Italy; CMNH, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA; MNHN, Muséum National d'Histoire Naturelle, Paris, France; MZL, Museum of Zoology and Entomology, Lund, Sweden; MZUF, Museo Zoologico "La Specola," Firenze, Italy; ZMB, Museum für Naturkunde der Humboldt-Universität, Berlin, Germany; ZMC, Zoologisk Museum, Copenhagen, Denmark.

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Submitted 23 April 1996.

Subfamily Brentinae

Tribe Brentini

Debora forficata (J. Thomson)

Debora forficata: Damoiseau, 1967a:342; Damoiseau, 1972:268.

Specimens Examined.—EQUATORIAL GUINEA. Mongo, 12 Jun 1947, one male (Palau, ex coll. Frieser; CLB).

Locality Records.—This species is known from Ivory Coast, Ghana, Cameroon, Gabon, and People's Republic of Congo; this is the first record for Equatorial Guinea.

Spatherhinus ophthalmicus Kolbe

Spatherhinus ophthalmicus: Damoiseau, 1967a:347.

Specimens Examined.—CAMEROON. Likomba, evening, at light, 11 Feb 1938, one specimen (Buhr; ZMB); Lokom, 10 Sep 1990, one male (Mourgliä; CLB).

Locality Records.—This species is known from Gabon and People's Republic of Congo; this is the first record for Cameroon.

Pericordus freyi Damoiseau

Pericordus freyi: Damoiseau, 1967a:379.

Specimens Examined.—ZAMBIA. Southern Province: Lusaka, Kafue River, Kafue city, 1200 m, Dec 1985, one male and one female (Ferrero; CLB).

Locality Records.—This species is known from Mozambique and South Africa; this is the first record for Zambia.

Symmorphocerus approximatus Damoiseau

Symmorphocerus approximatus: Damoiseau, 1967a:382; Damoiseau, 1967c:130.

Specimens Examined.—GABON. Ogové R. (= Ogooué River), one female (Good, ex coll. Holland; CMNH).

Locality Records.—This species is known from Republic of Guinea, People's Republic of Congo, and Angola; this is the first record for Gabon.

Symmorphocerus alluaudi Senna

Symmorphocerus alluaudi: Damoiseau, 1967a:385; Quentin, 1970:219.

Specimens Examined.—GAMBIA. About 5 km SSW Gunjur, oil palm and mangrove veg., close to the beach, at light, (18.45–20.30), UTM 28PCK0554, loc. 8, 13 Nov 1977, one female (Cederholm, Danielsson, Hammarstedt, Hedqvist, Samuelsson; MZL). BURKINA FASO. Ouest: Bobo Dioulasso, Oct 1982, one male (Politrapp, ex coll. Frieser; CLB). TOGO. Region Centrale: Fazao (580 m), 16 Apr 1985, one female (Mourgliä; CLB). KENYA. Machakos: Kibwezi, Nov 1905, two specimens (Schefler; ZMB).

Locality Records.—This species is known from Senegal, Ivory Coast, Nigeria, and People's Republic of Congo; these are the first records for Gambia, Burkina Faso, Togo, and Kenya. The record from Kenya is also the first one of this taxon for East Africa (Fig. 1).



Fig. 1.—Distribution of *Symmorphocerus alluaudi* Senna. Triangles: previous records; circles: new records.

Afrocordus vicarius (Kleine)

Cordus vicarius: Damoiseau, 1967a:396; Damoiseau, 1967b:12; Damoiseau, 1975:60.

Afrocordus vicarius: Damoiseau, 1980:31; Bartolozzi and Osella, 1990:241.

Specimens Examined.—GABON. Ogové R. (= Ogooué River), one male (Good, ex coll. Holland; CMNH).

Locality Records.—This species is known from Senegal, Republic of Guinea, Sierra Leone, Ivory Coast, Benin, People's Republic of Congo, Zaire, Angola, Tanzania, and Malawi; this is the first record for Gabon.



Fig. 2.—Distribution of *Hemicordus ivorensis* Damoiseau. Triangle: previous records; circles: new records.

Hemicordus ivorensis Damoiseau

Hemicordus ivorensis Damoiseau, 1980:28.

Specimens Examined.—SIERRA LEONE. W. Area: Freetown, S. Michel Lodge near Lakta, 9–24 Jun 1988, one female (Mourgliia; CLB). TOGO. Ouest: Fazao (580 m), 16 Apr 1985, one male (Mourgliia; CLB). CAMEROON. Johann-Albrechts-Höhe, 10 Apr 1898, one specimen (ZMB); same locality, Jul–Aug 1897, one specimen (Conradt; ZMB).

Locality Records.—This species was known only from Ivory Coast; these are the first records for Sierra Leone, Togo, and Cameroon. These new data greatly extend the range of this brentid to the east and west (Fig. 2).

Perisymphocerus latirostris (Power)

Perisymphocerus latirostris: Damoiseau, 1967a:401; Damoiseau, 1968:172; Damoiseau, 1972:268; Bartolozzi, 1991:19.

Specimens Examined.—GAMBIA. About 5 km SSW Gunjur, oil palm and mangrove veg., close to the beach, at light (18.45–20.30), UTM 28PCK0554, loc. 8, 13 Nov 1977, one male (Cederholm, Danielsson, Hammarstedt, Hedqvist, Samuelsson; MZL); 3.5 km S Georgetown, hilltop at Sankuli Kunda, about 30 m, at light (18.30–20.15), UTM 28PEK2593, loc. 37, 15 Nov 1977, one male (Cederholm, Danielsson, Hammarstedt, Hedqvist, Samuelsson; MZL); Tanji River, 3 km SW Brufut, at light (19.00–21.00), UTM 28PCK087773, loc. 9, 20 Feb 1977, one female (Cederholm, Danielsson, Hammarstedt, Hedqvist, Samuelsson; MZL).

Locality Records.—This species is known from Senegal, Equatorial Guinea, Ivory Coast, Ghana, Togo, Nigeria, Sudan, and Ethiopia; this is the first record for Gambia.

Micramorphocephalus consobrinus Kleine

Micramorphocephalus consobrinus: Damoiseau, 1967a:409; Damoiseau, 1972:268.

Specimens Examined.—REPUBLIC OF GUINEA. Nimba Mts., Mifergui (700 m), at light, 6 May 1993, one female (Perrin; MNHN).

Locality Records.—This species is known from Senegal, Sierra Leone, Ivory Coast, Ghana, People's Republic of Congo, and Central African Republic; this is the first record for the Republic of Guinea.

Hadramorphocephalus calvei (Power)

Hadramorphocephalus calvei: Damoiseau, 1967a:411.

Specimens Examined.—MALI. Azaouâd: Timbuctù (= Tombouctou), 17 Aug 1927, one male and one female (Madsen; ZMC).

Locality Records.—This species is known from Senegal and Chad; this is the first record for Mali.

Tribe Cyphagogini

Cormopus guineensis Damoiseau

Cormopus guineensis Damoiseau, 1967a:38.

Specimens Examined.—CAMEROON. Littoral: 25 km WNW Douala, Modeka, loc. 27, secondary forest and plantation, at light, 18 Jan 1978, one specimen (Gardenfors, Hall, and Samuelsson; MZL).

Locality Records.—This species was known only from Guinea; this is the first record for Cameroon.

Phobetromimus simulans Kleine

Phobetromimus simulans: Damoiseau, 1967a:60; Damoiseau, 1972:260; Bartolozzi and Osella 1990: 234.

Specimens Examined.—RWANDA. Cyangugu pref.: Nyakabuye, 25 Dec 1982, one specimen (Mühle; CLB).

Locality Records.—This species is known from Republic of Guinea, Sierra Leone, Ivory Coast, Ghana, Cameroon, People's Republic of Congo, and Tanzania; this is the first record for Rwanda.

Adidactus cancellatus (Lacordaire)

Adidactus cancellatus: Damoiseau, 1967a:67; Quentin, 1970:209; Damoiseau, 1972:261; Sforzi, 1992:3.

Specimens Examined.—REPUBLIC OF GUINEA. Seredou, at light, 16 May 1975, one specimen (Zott; ZMB). NAMIBIA. *East Caprivi*: Mudumu Nat. Park, Nakatwa, (18°10'S–23°26'E), at light, 8–13 Mar 1992, one specimen (Exp. ZMB 1992, Uhlig; ZMB).

Locality Records.—This species is known from Ivory Coast, Ghana, Cameroon, Gabon, People's Republic of Congo, and Tanzania; these are the first records for the Republic of Guinea and Namibia.

Xestocoryphus intermedius Damoiseau

Xestocoryphus intermedius Damoiseau, 1967a:91; Damoiseau, 1972:261; Bartolozzi, 1991:4.

Specimens Examined.—CAMEROON. Johann-Albrechts-Höhe, one specimen (Conradt; ZMB).

Locality Records.—This species is known from Ghana, Zaire, and Tanzania; this is the first record for Cameroon.

Xestocoryphus decellei Damoiseau

Xestocoryphus decellei Damoiseau, 1967a:94.

Specimens Examined.—CAMEROON. *Sud Province*: Lolodorf, Dec 1914, one specimen (Good; CMNH).

Locality Records.—This species is known from Republic of Guinea and Ivory Coast; this is the first record for Cameroon.

Rhytidopterus compressithorax (Senna)

Rhytidopterus compressithorax: Damoiseau, 1967a:103.

Specimens Examined.—RWANDA. *Cyangugu pref.*: Nyakabuye, 24 May 1984, one specimen (Mühle; CLB); same locality, 1–17 Feb 1983, one specimen (Mühle; CLB); Gishoma, 20 Feb 1983, one specimen (Mühle; CLB).

Locality Records.—This species is known from Ivory Coast, Cameroon, Equatorial Guinea, People's Republic of Congo, and Sudan; this is the first record for Rwanda.

Podozemius mustus Kolbe

Podozemius mustus: Damoiseau, 1967a:111.

Specimens Examined.—SOUTH AFRICA. *Natal*: Tugela River, Starger, Jan 1989, one specimen (Werner; CLB).

Locality Records.—This species is known from Ivory Coast, Cameroon, Equatorial Guinea, Gabon, and People's Republic of Congo; this is the first record for South Africa.

Podozemius kolbei (Kleine)

Podozemius kolbei: Damoiseau, 1967a:113; Damoiseau, 1967b:5; Damoiseau, 1967c:126; Damoiseau, 1968:169; Quentin, 1970:210; Damoiseau, 1972:263; Damoiseau, 1975:56.

Specimens Examined.—GAMBIA. Bathurst, Jan 1968, one specimen (Palm; MZL). RWANDA. *Cyangugu pref.*: Nyakabuye, 15–30 Nov 1982, three specimens (Mühle; CLB).

Locality Records.—This species is known from Ivory Coast, Ghana, Togo,

Nigeria, Cameroon, Equatorial Guinea, People's Republic of Congo, Angola, Sudan, Ethiopia, and Tanzania; these are the first records for Gambia and Rwanda.

Anomalopleura babaulti (De Muizon)

Anomalopleura babaulti: Damoiseau, 1967a:117.

Specimens Examined.—REPUBLIC OF GUINEA. Seredou, 4 Apr 1975, one specimen (Zott; ZMB).

Locality Records.—This species was known only from People's Republic of Congo; this is the first record for the Republic of Guinea.

Zemioses rufostriatus (Kleine)

Zemioses rufostriatus: Damoiseau, 1967a:153.

Specimens Examined.—RWANDA. *Cyangugu pref.*: Nyakabuye, 24 May 1984, five specimens (Mühle; CLB).

Locality Records.—This species is known from Ivory Coast, Cameroon, Equatorial Guinea, and People's Republic of Congo; this is the first record for Rwanda.

Tribe Stereodermini

Cerobates (*Cerobates*) *conveniens* Kleine

Cerobates (*Cerobates*) *conveniens*: Damoiseau, 1967a:205; Damoiseau, 1967b:8; Quentin, 1970:214; Damoiseau, 1972:265; Bartolozzi and Sforzi, 1994:250.

Specimens Examined.—SENEGAL. *Casamance*: 1 km NE Djibelor, about 7.5 km SW Ziguinchor, in forest, at light (19.00–21.00), UTM28PCJ5687, loc. 29, 9 Dec 1977, one specimen (Cederholm, Danielsson, Hammarstedt, Hedqvist, Samuelsson; MZL). CAMEROON. *SW Province*: Fako distr., Bomana, about 11 km N Idenau, 300–400 m, (4°13' N–9°4' E), under bark, 21 Jul 1984, two specimens (Davidson; CMNH).

Locality Records.—This species is known from Ivory Coast, Ghana, Equatorial Guinea, People's Republic of Congo, Zaire, and Kenya; these are the first records for Senegal and Cameroon.

Cerobates (*Cerobates*) *corruptus* Kleine

Cerobates (*Cerobates*) *corruptus*: Damoiseau, 1967a:192; Damoiseau, 1967b:8; Bartolozzi and Sforzi, 1994:250.

Specimens Examined.—CAMEROON. *Sud Province*: Lolodorf, Sep 1913, one specimen (Good; CMNH). GABON. Kangvé, Ogové R. (= Ogooué River), one specimen (Good; CMNH).

Locality Records.—This species is known from People's Republic of Congo, Zaire, Kenya, Tanzania, and Mozambique; these are the first records for Cameroon and Gabon.

Cerobates (*Cerobates*) *cruentatus* Senna

Cerobates (*Cerobates*) *cruentatus*: Damoiseau, 1967a:191; Damoiseau, 1967b:8; Quentin, 1970:213; Damoiseau, 1972:264; Bartolozzi and Osella, 1990:236; Bartolozzi, 1991:6; Bartolozzi and Sforzi, 1994:250.

Specimens Examined.—GABON. *Moyen Ogoove*: Lambarené, one specimen (Good; CMNH).

Locality Records.—This species is known from Ivory Coast, Ghana, Cameroon, Equatorial Guinea, People's Republic of Congo, Zaire, Uganda, Rwanda, and Kenya; this is the first record for Gabon.

Cerobates (Jonthocerus) burgeoni De Muizon

Cerobates (Jonthocerus) burgeoni: Damoiseau, 1967a:182; Bartolozzi and Osella, 1990:287.

Specimens Examined.—SIERRA LEONE. *Northern Province*: between Sinikoro and Kondembaia, 3 Dec 1984, one male (Rossi; CLB).

Locality Records.—This species is known from Ghana and People's Republic of Congo; this is the first record for Sierra Leone.

Cerobates (Jonthocerus) elegans Damoiseau

Cerobates (Jonthocerus) elegans: Damoiseau, 1967a:184; Damoiseau, 1967b:6; Damoiseau, 1967c:127; Damoiseau, 1972:264; Bartolozzi, 1991:8.

Specimens Examined.—REPUBLIC OF GUINEA. Seredou, at light, 4 Apr 1975, one specimen (Zott; ZMB).

Locality Records.—This species is known from Ghana, Cameroon, People's Republic of Congo, Zaire, Angola, and Uganda; this is the first record for the Republic of Guinea.

Tribe Trachelizini

Microtrachelizus fractus Kleine

Microtrachelizus fractus: Damoiseau, 1967a:225.

Specimens Examined.—CAMEROON. *Sud Province*: 15 km E Ebolowa Keeke, loc. 15, secondary forest with cocoa plantation, at light, 5 Jan 1978, two specimens (Gardenfors, Hall, Samuelsson; MZL).

Locality Records.—This species is known from People's Republic of Congo; this is the first record for Cameroon.

Pseudoceocephalus formosus Kleine

Pseudoceocephalus formosus: Damoiseau, 1967a:264; Damoiseau, 1967b:13; Damoiseau, 1972:267.

Specimens Examined.—CAMEROON. Johann-Albrechts-Höhe, 3–28 Aug 1898, three specimens (ZMB); same locality, 11 Apr–27 May 1898, one specimen (Conradt; ZMB). REPUBLIC OF GUINEA. Seredou, at light, 16 Apr 1975, one specimen (Zott; ZMB).

Locality Records.—This species is known from Ghana, Gabon, and People's Republic of Congo; these are the first records for the Republic of Guinea and Cameroon.

Pseudomygaleicus grandis (Damoiseau)

Pseudomygaleicus grandis: Damoiseau, 1967a:275; Damoiseau, 1967c:128.

Specimens Examined.—EQUATORIAL GUINEA. *Subregion unknown*: one specimen (Tessman; ZMB).

Locality Records.—This species is known from Ivory Coast, Central African Republic, People's Republic of Congo, Zaire, and Angola; this is the first record for Equatorial Guinea.

Pseudomygaleicus surdus Damoiseau

Pseudomygaleicus surdus Damoiseau, 1967a:281; Damoiseau, 1975:59.

Specimens Examined.—BENIN. *Borgou*: Parakou, 5–24 Jul 1989, one specimen (van Vondel; CBJV).

Locality Records.—This species is known from Ivory Coast, Angola, and Uganda, this is the first record for Benin.

Gynandrorhynchus tarsalis (Kleine)

Gynandrorhynchus tarsalis: Damoiseau, 1967a:294; Damoiseau, 1972:267; Damoiseau, 1975:58; Bartolozzi, 1991:14.

Specimens Examined.—REPUBLIC OF GUINEA. Nimba Mts., Bossou (550 m), (on dead *Ficus* sp.), 5 May 1993, one specimen (Perrin; MNHN). CAMEROON. Efulen, Oct–Nov 1913, 23 specimens (Weber; CMNH). GABON. *Ogoove Maritime*: Batanga, one specimen (Good; CMNH). RWANDA. *Cyangugu pref.*: Nyakabuye, 20 Jul 1984, one specimen (Mühle; CLB).

Locality Records.—This species is known from Ivory Coast, Ghana, Zaire, Angola, and Tanzania; these are the first records for Republic of Guinea, Cameroon, Gabon, and Rwanda.

Gynandrorhynchus audax (Kleine)

Gynandrorhynchus audax: Quentin, 1966:1641; Damoiseau, 1967a:296.

Specimens Examined.—CAMEROON. Johann-Albrechts-Höhe, 14 Sep–6 Oct 1898, one specimen (Conradt; MZB); same locality, 11 Apr–27 May 1898 one specimen (Conradt; MZB); same locality, 30 Jan 1898, one specimen (Conradt; MZB).

Locality Records.—This species is known from Ivory Coast, People's Republic of Congo, Zaire, and Mozambique; this is the first record for Cameroon.

Anampyx edentulus Damoiseau

Anampyx edentulus: Damoiseau, 1967a:308.

Specimens Examined.—CAMEROON. Nasanakang, one specimen (Diehl; ZMB); *Sud Province*: Lolodorf, 8 Feb–27 Mar 1895, one specimen (Conradt; ZMB); Efulen, 28 Nov–29 Dec 1911/12, eight specimens (Weber; CMNH).

Locality Records.—This species is known from People's Republic of Congo; this is the first record for Cameroon.

Eumecopodus longicornis Calabresi

Eumecopodus longicornis: Damoiseau, 1967a:318.

Specimens Examined.—CAMEROON. Efulen, 6 Feb 1912, one female (Weber; CMNH).

Locality Records.—This species is known from People's Republic of Congo and Tanzania; this is the first record for Cameroon.

Eumecopodus burgeoni De Muizon

Eumecopodus burgeoni: Damoiseau, 1967a:320.

Specimens Examined.—GABON. *Moyen Ogoove*: Lambarené, one female (Good, ex coll. Holland; CMNH).

Locality Records.—This species is known from Republic of Guinea and People's Republic of Congo; this is the first record for Gabon.

Phitoderes gestroi Calabresi

Phitoderes gestroi: Damoiseau, 1967a:323; Bartolozzi and Osella, 1990:239.

Specimens Examined.—CAMEROON. *Sud Province*: Lolodorf, Feb 1914, one male (Good; CMNH); Efulen, Sep 1909 and 5 Dec 1913, two females (Weber; CMNH).

Locality Records.—This species is known from Sierra Leone, Ivory Coast, Equatorial Guinea, Gabon, and People's Republic of Congo; this is the first record for Cameroon.

Thoracobrenthus semistriatus Damoiseau

Thoracobrenthus semistriatus: Damoiseau, 1967a:326.

Specimens Examined.—CAMEROON. *Sud Province*: Lolodorf, Nov 1914, one specimen (Good; CMNH); Metet, Apr 1918, one specimen (Good; CMNH); without locality, 5 Apr 1910, one specimen (Weber; CMNH).

Locality Records.—This species is known from Ivory Coast and People's Republic of Congo; this is the first record for Cameroon.

Heterothesis elegans Kleine

Heterothesis elegans: Damoiseau, 1967a:332; Damoiseau, 1967c:129.

Specimens Examined.—GABON. Ogové R. (= Ogooué River), 12 males (Good, ex coll. Holland; CMNH).

Locality Records.—This species is known from Cameroon, People's Republic of Congo, and Angola; this is the first record for Gabon.

Paryphobrenthus latirostris (Gerstäcker)

Paryphobrenthus latirostris: Damoiseau, 1967a:334; Damoiseau, 1968:171; Sforzi, 1992:5.

Specimens Examined.—ANGOLA. *Huila distr.*: Mulondo (3600 ft), 23 Nov 1930, one male (CMNH). SOUTH AFRICA. *NE Transvaal*: Ofcolaco, Makhutswe River, Jan 1989, one female (Werner; CLB).

Locality Records.—This species is known from Zaire, Sudan, Tanzania, and Mozambique; these are the first records for Angola and South Africa.

Tribe Atopobrentini (sensu Damoiseau, 1967a)

Neoceocephalus freyi De Muizon

Neoceocephalus freyi: Damoiseau, 1967a:241; Bartolozzi, 1991:9; Bartolozzi and Sforzi, 1994:251.

Specimens Examined.—ZAMBIA. Nmkande, Nov 1973, three specimens (Piacenza; CGO, CLB).

Locality Records.—This species is known from Zaire, Kenya, Tanzania, Mozambique, and South Africa; this is the first record for Zambia.

Neoceocephalus punctatus Damoiseau

Neoceocephalus punctatus: Damoiseau, 1967a:247; Damoiseau, 1972:266.

Specimens Examined.—REPUBLIC OF GUINEA. Seredou, at light, 4 Apr 1975, one specimen (Zott; ZMB).

Locality Records.—This species is known from Ghana, Cameroon, Gabon, and People's Republic of Congo; this is the first record for the Republic of Guinea.

Neoceocephalus fausti (Senna)

Neoceocephalus fausti: Damoiseau, 1967a:251; Damoiseau, 1975:58.

Specimens Examined.—REPUBLIC OF GUINEA. Seredou, at light, 4 Apr 1975, two specimens (Zott; ZMB).

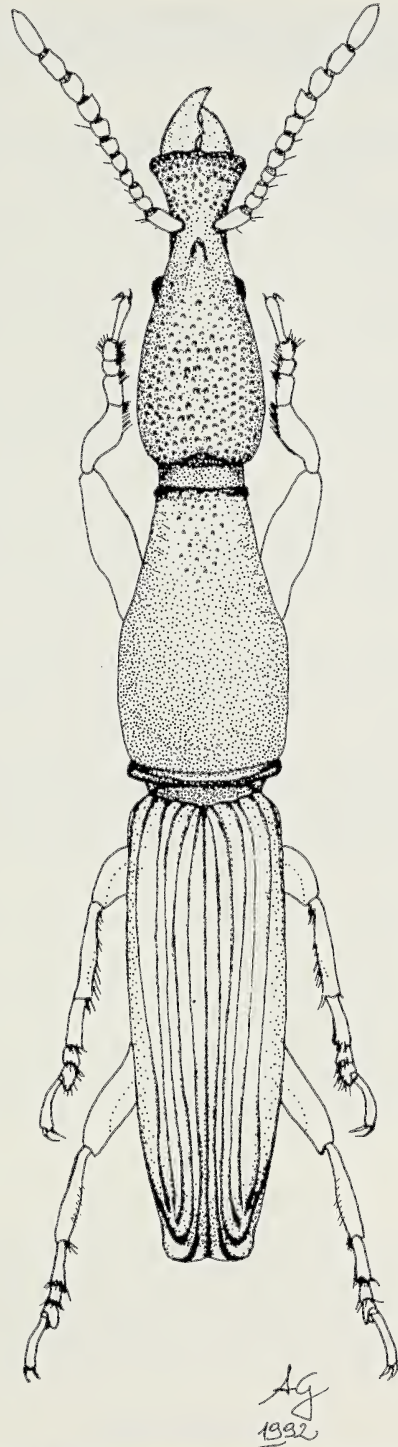


Fig. 3.—*Plesiobolbus sagax* Kolbe: habitus (total length 16.1 mm).

Locality Records.—This species is known from Ivory Coast, Cameroon, People's Republic of Congo, Angola, and South Africa (Transvaal); this is the first record for the Republic of Guinea.

Tribe Taphroderini (sensu Damoiseau, 1967a)

Plesiobolbus sagax Kolbe

Plesiobolbus sagax: Damoiseau, 1967a:463; Bartolozzi, 1991:26.

Specimens Examined.—CAMEROON. Efulen, Nov 1913, one male (Weber; CMNH).

Taxonomy and Distribution.—This species was briefly described by Kolbe in 1916, but Damoiseau (1967a) questioned the validity of this taxon and even the genus *Plesiobolbus* Kolbe. His statement was based on the fact that the types of the two species of *Plesiobolbus* (*P. sagax* and *P. cribriceps* Kolbe) could not be found, and Damoiseau never saw any African Taphroderinae with the characters of the genus. Two specimens in the Museum of Tervuren identified as *Plesiobolbus* by the well-known German specialist Kleine, were in fact females of the widespread species *Anisognathus czikii* Bolkay (Damoiseau, 1967a:463). Bartolozzi (1991) confirmed the validity of the genus *Plesiobolbus* and described the new species *P. martini* from Tanzania. In the material of CMNH there is a male specimen of *P. sagax*, the first to be found after Kolbe's short description of the species. The specimen agrees well with the short diagnosis of Kolbe, although its length (16.1 mm) is much greater than the type specimen of *P. sagax* (9.5 mm). It is useful to redescribe and illustrate this very rare and interesting insect.

Redescription.—Male: total length 16.1 mm, maximum width (at pronotum) 2.3 mm, antennae 3.9 mm. Body reddish brown with pronotum almost black (Fig. 3). Head longer than broad, with slightly rounded sides, well separated from neck. Occiput slightly projecting posteriorly on neck and bilobed. Temples longer than meta-, meso-, and prorostrum together. Upper surface covered with strong, shining granulation. Rostrum (length 2.4 mm). Metarostrum slightly shorter than distance between eyes, narrowing anteriorly; a fovea present between meta- and mesorostrum. Mesorostrum almost as long as metarostrum. Prorostrum as long as distance between eyes, enlarged anteriorly. Upper surface punctuated. Anterior border of prorostrum almost straight with very small projection in middle. Mandibles as long as prorostrum, acuminate, left one with tooth in middle. Pronotum as long as head and rostrum together, narrowed anteriorly. Surface smooth, dull, with sparse short golden pubescence; granulation on distal half of pronotal disc. Elytra shorter than pronotum and head together, narrowed posteriorly and narrower than pronotum. Upper surface convex; striae slightly punctuated, interstriae flattened with sparse short golden pubescence; interstriae 1, 2, and 3 elevated on declivity. Base of elytra slightly concave; each elytron apically rounded. Femora laterally compressed at base, unarmed. Underside reddish, shining, with golden pubescence only under rostrum. Two small longitudinal depressions laterally on mesorostrum. Small rounded foveola near base of head.

Female: unknown.

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THE BUTTERFLIES OF THE ISLE OF PINES, CUBA:
EIGHTY YEARS ONDAVID SPENCER SMITH¹LUIS ROBERTO HERNÁNDEZ²NEIL DAVIES³

ABSTRACT

This account extends the first substantial report of the butterflies of the Isle of Pines, which included 65 species collected for Carnegie Museum of Natural History during 1910, 1912, and 1913, from our fieldwork in 1975-1976 and 1993-1995. One hundred eleven species have now been reported from the island, and distributional data are presented for all recent records. The list includes 64% of the Cuban fauna recorded from less than 2% of the total land area of Cuba; proportional representation of taxonomic families and endemic taxa in Cuba are considered. The island comprises two distinct parts: the cultivated, populous, and severely damaged northern two-thirds, including hill ranges; the low, relatively undisturbed, dry forest of the southern one-third, separated by a swamp, the Ciénaga de Lanier. Species numbers for pooled localities north of the Ciénaga are comparable with those of the south, but diversity in the north is concentrated in very small species-rich enclaves. These northern sites are faunal relicts; they are vulnerable and they are unprotected, stressing the need for conservation of the southern forest zone. Wet and dry seasonality is considered, and the need for phenological data for further assessing the fauna is discussed. Origins of the fauna are considered in the context of lack of phenotypic divergence between Isle of Pines and main-island populations, and the late Pleistocene is proposed as a major colonization period, with continuing two-way dispersive interchange across the Gulf of Batabanó viewed as probable. Genetic analysis of three species shows close correspondence between Isle of Pines and main island populations. The fauna is compared with that of Cuba, in general, and of an ecologically equivalent region of western Cuba, in particular.

KEY WORDS: Cuba, genetic analysis, Hesperioidea, Papilionoidea, phenology, Pleistocene, relict populations, zoogeography

INTRODUCTION

Topography and Climate

The Isle of Pines (Isla de la Juventud) lies off the southwestern coast of Cuba, due south of the boundary between the provinces of La Habana and Pinar del Río, and is independently administered by the central government. Separated from the main island by the shallow Gulf of Batabanó, the closest approach is ca. 51 km. Its land area is ca. 2200 km², or less than 2% of the area of the main island. The island is geologically and ecologically composed of two very different parts. The northern two-thirds of the island (ca. 1350 km²) is Jurassic in age

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(Lewis and Draper, 1990), some parts formerly bearing extensive forests of pine (*Pinus occidentalis*), and includes three main groups of hills of which the highest point is just over 310 m at Pico La Cañada. This region is plentifully supplied with rivers. In contrast, the southern one-third of the island (ca. 770 km²), the Llanura Cársica del Sur, is of low elevation, of late Pleistocene age (Webb, personal communication), and covered with dry, largely undisturbed semideciduous limestone forest. The difference between the two regions is so dramatic that several early maps suggested two islands instead of one (Jiménez, 1976). The two regions are linked by the Ciénaga de Lanier, a fresh-to-brackish swamp oriented east to west and open to the sea through mangrove at either end, irregular in outline, and without precise limits but covering an estimated 80 km² (Fig. 1).

A summary of climate has been provided by Gort et al. (1994) based on records from 1975 to 1987. In common with western Cuba, the Isle of Pines has a well-defined dry season from November through April, and wet season from May through October. The wettest months are June and September (each with 207 mm) and the driest December (34 mm) and March (31 mm). The mean annual temperature is 25.4°C, with maximum and minimum monthly means (July and February) of 27.9°C and 18.3°C. In April and May strong, dry southerly winds reach the island, backing to easterly or southeasterly during summer; at other times winds are predominantly easterly, inclining to northeasterly in winter.

Historical Background

The Isle of Pines had a long history of indigenous, pre-Hispanic Taino presence, but the subsequent history of colonization is both complex and unusual, being almost restricted to the northern part of the island. After 1576, when the island was placed by Crown Grant into the hands of Jerónimo de Rojas y Avellaneda, the region north of the Ciénaga de Lanier was settled for cattle raising and agriculture, although remaining thinly populated. Around 1760, almost the entire northern area was purchased by Nicolás Duarte and divided into seven circular haciendas or *hatos*, later subdivided into smaller farms (Jiménez, 1976). From the late 16th to the early 19th centuries the island was regularly visited for water and food by a succession of French, Dutch, and English pirates and freebooters.

A summary of the more recent history of the island is essential for understanding its cartography and locality records of early butterfly collections, mentioned below. The main town of Nueva Gerona was founded in 1830, Santa Fé (La Fé) soon after, and throughout the 19th century, the north of the island supported a small population, principally of subsistence farmers and fishermen of Cuban and Spanish origin. A dramatic change in the colonization pattern followed the Spanish-American War of 1898. Although Cuban independence was established by the United States Congress in 1902, Article 6 of the Platt Amendment excluded the Isle of Pines from Cuban jurisdiction, "the title of ownership thereof being left to future adjustment by treaty." Formal attachment of the Isle of Pines to Cuba was delayed until 1925. In the interim, the island was de facto open to the United States; extensive areas of the northern two-thirds of the island were purchased by North American entrepreneurs from the Spanish and Cuban owners and divided into parcels offered for citrus cultivation. While many were purchased by North Americans, only some 400 colonists actually arrived to work the land. These rectangular plots dominate maps of the period (e.g., Giltner, 1904), together with the new riverside settlements established by the immigrants. The most notable of

sites including Candel, Palma Alta, El Jorobada, Acosta, and Llevat. On the southwest coast the small settlement of Jacksonville was established around 1904 by colonists from Grand Cayman Island; now named Cocodrilo, this village has a population of about 200. Isolated cottages are situated at Hato Milián, Siguanea, Rincón de Guanál, and Playa Blanca, and a meteorological radar station is established at Punta del Este. Between 1920 and 1930 the village of Carapachibey comprised 20–30 dwellings of charcoal burners; this village has vanished but a modern lighthouse was built nearby.

Entomological Studies

Field studies on the insects of the Isle of Pines have been carried out on sporadic and long-separated visits. The first records of the island's butterflies, some 13 species, were published by Poey (1854*a*, 1854*b*, 1861) from specimens collected by Juan Gundlach during a two-week stay early in 1854, when the celebrated naturalist also obtained land snails, reptiles, and birds. Over half a century later, expeditions from Carnegie Museum of Natural History provided the foundation of knowledge of the island's biotas; in some instances these remain the only source of information. The first extensive insect collections were made J. L. Graf and G. A. Link, members of an expedition in the spring of 1910, and later by Link, who returned to the island from early 1912 to June 1913. An account that included some 65 butterfly species was published by Holland (1916), and reports on other groups followed: the Orthoptera (Holland and Kahl, 1916; Bruner, 1919), Odonata (Kahl, 1916), Rhynchota [i.e., Hemiptera–Heteroptera] (Heide-mann and Osborn, 1917), Hymenoptera (Rohwer and Holland, 1917), and Coleoptera (Holland and Schwarz, 1917). Locality labels on this butterfly material in Carnegie Museum show that over 90% were collected at Nueva Gerona, and the remaining few were taken in the townships of Columbia, McKinley, Los Indios, and Santa Fé. The entire southern area is represented by only a single specimen of *Eurytides celadon* collected in 1912 at Calheta Grande, on the southwest coast. No additional localities are mentioned in accounts of other insects except for some beetles from "Caballos mountain" (Holland and Schwarz, 1917), a hill east of Nueva Gerona, and it is clear that the entomological collecting at that time centered on the new American settlements.

A few specimens of historical interest obtained during the early years of the century, prior to the Carnegie expeditions (Table 1), are preserved in museum collections. Specimens collected by a W. R. Zappey are held at the Harvard Museum of Comparative Zoology, Cambridge, Massachusetts, and data labels of others in the National Museum of Natural History, Washington, D.C., document collections made at Columbia in 1903 and 1913 by H. B. Hill. Other names attached to Isle of Pines specimens that bear no date include "Zappalorti" and "Palmer and Riley."

The fieldwork carried out on the Isle of Pines between 1910 and 1913 on behalf of Carnegie Museum was a remarkable contribution to knowledge of Cuba's butterfly fauna. The collections of Graf and Link enabled Holland (1916) to list 65 species, while noting that Link, who obtained most of the museum's specimens during over a year on the island, was primarily engaged in collecting birds and "...gathered specimens of such insects as he encountered at times when he was not otherwise engaged." Although Graf and Link worked almost exclusively outside the southern forest, the collection of butterflies published by Holland com-

prises over half the present count for the island. Here we present the first comprehensive account of the butterfly fauna of the island since 1916, with consideration of the present distribution, conservation status, possible origins, and relationship of the insular fauna to that of the main island of Cuba.

One of the present authors (LRH), with G. Alayón and L. Zayas, carried out fieldwork on bimonthly visits during 1975 and 1976, each of three to five days and covering every month, during a general survey of the island's insects. A few of the species newly recorded at this time were mentioned by Alayo and Hernández (1987) and all are included here. As part of a collaborative research program on butterfly diversity in Cuba between the National Museum of Natural History (Habana) and the Hope Entomological Collections (Oxford University), we recently have worked on the Isle of Pines on four visits: 3–8 July 1993 (LRH, DSS, ND), 24–28 March 1994 (LRH, DSS), 25–29 August 1994 (LRH, DSS), and 17–22 March 1995 (LRH, DSS). During these visits approximately one-third of the field time was spent south of the Ciénaga de Lanier and two-thirds in northern localities.

Botanical Studies

A short account of the plants of the island was prepared by Britton (1916); an extensive work by Jennings (1917) followed, based largely on the herbarium of Carnegie Museum. Jennings provided a survey of 19th century botanical collections; he also worked on the island with Link in May 1910, and his account also credits material obtained by Link at Nueva Gerona (May–June 1912) and Los Indios (November 1912). Jennings recorded 757 plant species and cited Britton's (1916) extrapolated estimate that "...the total natural flora of the island is not less than one thousand five hundred species." The same figure has been given recently for the higher plant taxa of the Isle of Pines (Gort et al., 1994). A general account of the phytogeographic zones of Cuba, including the Isle of Pines, is provided by Samek (1973).

TABULATION OF RECORDS

Nature of Records

We have no ecological information on the localities in which Link and Graf collected the material published by Holland (1916), other than noting that virtually all were obtained north of the Ciénaga de Lanier. It is unlikely that any of their localities have survived, and therefore in this work all 1910–1913 records are grouped together (Table 1). In tabulating the 1975–1976 records, all localities north of the Ciénaga have been grouped together and separated from those of the southern forest (Table 1). Most of the former localities were resurveyed in 1993–1995, but the two data sets, obtained 20 years apart, are not strictly comparable. First, intensive and complete listing of butterfly species was not a primary objective of the earlier survey; and second, continuing habitat degradation over the two decades has changed or obliterated some sites. Notably, western coastal localities, the Sierra de La Cañada, and the white-sand zone of Los Indios were considerably less damaged and more species-rich in 1975–1976 than during recent visits. However, records south of the Ciénaga for 1975–1976 and 1993–1995 are directly comparable; habitats surveyed during both periods were essentially unchanged, but the area west of Cocodrilo (Fig. 1) was not visited in the earlier work. Localities north of the Ciénaga are arranged in three approximate geograph-

Table 1.—*Tabulated butterfly records (+) from the Isle of Pines including: 1910–1913 collections for Carnegie Museum in Holland (1916) with three early records (++) from other sources (see Results and Discussion); 1975–1976 records from south of the island, with the remainder of localities grouped together; 1993–1995 records tabulated in geographic zones (North, East, West, South). s: sight record. Localities are described in Tabulation of Records and shown in Figure 1. Taxonomic notes clarifying listings in Holland (1916) are given in the Results and Discussion section.*

Taxon	1910–1913	1975–1976		1993–1995			
		Other	South	North	East	West	South
Danaidae							
<i>Danaus eresimus tethys</i> (Forbes)							+
<i>Danaus gilippus berenice</i> (Cramer)	+	+	+	+	+	+	+
<i>Danaus plexippus</i> (Linnaeus)		+	+		+		+
<i>Anetia briarea numidia</i> (Hübner)		+		s			
Satyridae							
<i>Calisto h. herophile</i> (Hübner)	+	+	+	+	+	+	+
<i>Calisto sibylla smintheus</i> (Bates)		+					
Nymphalidae							
<i>Doxocopa laure druryi</i> (Hübner)		+	+	+	+		+
<i>Asterocampa idyia</i> (Geyer)		+	+				
<i>Siderone galanthis nemesis</i> (Ill.)	+		+	+	+	+	+
<i>Memphis e. echemus</i> (Doubleday)			+				
<i>Marpesia e. eleuchea</i> (Hübner)	+	+	+	+	+	+	+
<i>Marpesia chiron</i> (Fabricius)		+					
<i>Colobura dirce</i> (Linnaeus)		+			+		+
<i>Historis o. odius</i> (Fabricius)	+	+	+	+	+		+
<i>Historis acheronta semele</i> (Bates)					+		
<i>Hamadryas amphicloe diasia</i> (Fruh.)		+					
<i>Lucinia s. sida</i> (Hübner)	+				+		+
<i>Eunica tatila tatilista</i> (Kaye)			+	+	+		+
<i>Eunica monima</i> (Cramer)	++			+	+		+
<i>Adelpha iphicla iphimedia</i> (Fruh.)	+		+	+	+	+	+
<i>Junonia c. coenia</i> (Hübner)	+		+	+	+	+	+
<i>Junonia evarete</i> (Stoll)	+	+	+				+
<i>Junonia genoveva</i> (Cramer)		+		+	+	+	+
<i>Anartia jatrophae guantanamo</i> (Munr.)	+	+	+	+	+	+	+
<i>Anartia chrysopelea</i> (Hübner)	+	+					
<i>Siproeta stelenes biplagiata</i> (Fruh.)	+	+	+	+	+	+	+
<i>Phyciodes phaon</i> (Edwards)		+	+				+
<i>Anthanassa frisia</i> (Poey)	+		+	+			+
<i>Euptoieta h. hegesia</i> (Cramer)	+	+	+	+	+		+
Heliconiidae							
<i>Heliconius charitonia ramsdeni</i> (Comstock & Brown)	+	+	+	+	+	+	+
<i>Dryas iulia nudeola</i> (Bates)	+	+	+	+	+	+	+
<i>Agraulis vanillae insularis</i> (Maynard)	+	+	+	+	+	+	+
Libytheidae							
<i>Libytheana motya</i> (Boisd. & Lec.)	++		+	+		+	+
Lycaenidae							
<i>Eumaeus atala</i> (Poey)	+	+				+	
<i>Allosmaitia c. coelebs</i> (H-Schäffer)				+			+
<i>Strymon martialis</i> (H-Schäffer)	+				+		+
<i>Strymon limenia</i> (Hewitson)							+
<i>Strymon columella cybira</i> (Hew.)	+			+	+	+	+
<i>Electrostrymon a. angelia</i> (Hew.)	+	+		+	+		+
<i>Leptotes cassius theonus</i> (Lucas)	+	+		+	+	+	+
<i>Hemiargus hanno filenus</i> (Poey)	+	+	+	+	+	+	+
<i>Nesiostrymon c. celida</i> (Lucas)	++						
<i>Cyclargus a. ammon</i> (Lucas)	+	+	+	+	+	+	+
<i>Brephidium exilis isophthalma</i> (H-S.)			+				

Table 1.—Continued.

Taxon	1910- 1913	1975-1976		1993-1995			
		Other	South	North	East	West	South
Pieridae							
<i>Ascia monuste eubotea</i> (Godart)	+	+	+	+	+	+	+
<i>Appias drusilla poeyi</i> (Butler)	+	+		+	+	+	+
<i>Eurema nise</i> (Cramer)		+	+	+	+		+
<i>Eurema daira palmira</i> (Poey)	+	+	+	+	+	+	+
<i>Eurema lisa</i> (Boisduval & Leconte)	+	+	+	+	+	+	+
<i>Eurema lucina</i> (Poey)	+			+	+		
<i>Eurema amelia</i> (Poey)	+		+				
<i>Eurema messalina</i> (Fabricius)	+			+	+	+	+
<i>Durema d. dina</i> (Poey)	+	+	+	+	+		+
<i>Eurema boisduvaliana</i> (C. & R. Felder)					+		
<i>Eurema proterpia</i> (Fabricius)					+		+
<i>Eurema nicippe</i> (Cramer)	+	+	+	+	+		+
<i>Nathalis iole</i> (Boisduval)		+	+				+
<i>Kricogonia lyside</i> (Godart)						+	
<i>Anteos maerula</i> (Fabricius)		+	+				
<i>Anteos clorinde</i> (Fruhstorfer)		+			+	+	
<i>Phoebis philea</i> (Linnaeus)					+	+	
<i>Phoebis argante fornax</i> (Butler)	+						
<i>Phoebis agarithe antillia</i> (Brown)		+	+	+	+		+
<i>Phoebis s. sennae</i> (Linnaeus)	+	+	+	+	+	+	+
<i>Aphrissa o. orbis</i> (Poey)	+	+					+
<i>Aphrissa neleis</i> (Boisduval)	+			+	+		+
<i>Aphrissa statira cubana</i> (D'Almeida)	+			+	+		+
Papilionidae							
<i>Battus polydamas cubensis</i> (Dufrane)		+	+	+	+		+
<i>Battus devilliers</i> (Godart)		+	+		+		
<i>Heraclides aristodemus temenes</i> (God.)		+					
<i>Heraclides androgeus epidaurus</i> (G. & S.)		+	+				+
<i>Heraclides a. andraemon</i> (Hübner)	+	+	+	+	+	+	+
<i>Heraclides caignuanabus</i> (Poey)		+	+	+	+		+
<i>Protesilaus celadon</i> (Lucas)	+	+					+
Hesperiidae							
<i>Phocides pigmalion batabano</i> (Luc.)	+		+				+
<i>Proteides mercurius sanantonio</i> (Luc.)	+			+	+		+
<i>Proteides maysi</i> (Lucas)	+			+	+		+
<i>Polygonus leo savigny</i> (Latreille)	+			+	+		+
<i>Urbanus proteus domingo</i> (Scudder)	+	+	+	+	+	+	+
<i>Urbanus dorantes santiago</i> (Lucas)	+	+	+	+	+	+	+
<i>Aguna asander haitensis</i> (Mab. & Boul.)	+	+	+		+		+
<i>Aguna claxon</i> (Evans)							+
<i>Astraptes anaphus anausis</i> (G. & S.)		+	+	+	+		
<i>Astraptes cassander</i> (Fabricius)	+	+					
<i>Astraptes h. habana</i> (Lucas)	+	+		+			+
<i>Astraptes talus</i> (Cramer)					+		
<i>Burca c. concolor</i> (H-Schäffer)						+	
<i>Gesta g. gesta</i> (Evans)					+		
<i>Achlyodes mithridates papinianus</i> (Poey)				+	+		+
<i>Ephyriades arcas philemon</i> (Fabr.)	+						
<i>Ephyriades b. brunnea</i> (H-Schäffer)	+			+	+		+
<i>Pyrgus o. oileus</i> (Linnaeus)	+	+	+	+	+	+	+
<i>Pyrrhocalles antiqua orientis</i> (Skin.)	+	+	+	+	+		+
<i>Perichares philetes</i> (Gmelin)				+			+

Table 1.—Continued.

Taxon	1910–1913	1975–1976		1993–1995			
		Other	South	North	East	West	South
<i>Synapte m. malitiosa</i> (H-Schäffer)				+			+
<i>Cymaenes tripunctus</i> (H-Schäffer)	+			+	+	+	+
<i>Oarisma nanus</i> (Herrich-Schäffer)	+	+					
<i>Hylephila phyleus</i> (Drury)	+	+	+	+			+
<i>Polites b. baracoa</i> (Lucas)	+			+			+
<i>Atalopedes m. mesogramma</i> (Latr.)	+			+			+
<i>Wallengrenia misera</i> (Lucas)	+			+	+		+
<i>Parachoranthus magdalia</i> (H-S.)							+
<i>Choranthus radians</i> (Lucas)		+	+	+	+	+	+
<i>Euhpyes c. cornelius</i> (Latreille)	+		+	+	+	+	+
<i>Asbolis capucinus</i> (Lucas)	+		+		+		+
<i>Panoquina sylvicola</i> (H-Schäffer)	+			+	+		+
<i>Panoquina corrupta</i> (H-Schäffer)	+			+	+		
<i>Panoquina o. ocola</i> (Edwards)	+						
<i>Panoquina p. panoquinoides</i> (Skinner)							+
<i>Nyctelius n. nyctelius</i> (Latr.)				+			+
<i>Lerodea eufala</i> (Edwards)	+	+		+			+

ical groups (north, east, west), and more detailed descriptions of these, and of localities south of the Ciénaga, are given below. Locality names and roads and tracks used in 1993–1995 are shown in Figure 1.

Northern Group

The principal northern locality was the forested region at El Abra (Fig. 2) near Nueva Gerona, at the southernmost end of the Sierra de Casas, together with adjoining tracks and fields. While it is probable that little primary forest remains even on the steeper slopes, areas of mature secondary forest are present. Other parts of this Sierra are largely deforested and marble quarrying is impacting the hills (Fig. 4). The El Abra locality has been notably species-rich on each visit, and accounts for most species recorded from the north. The forest on the nearby Sierra de Caballos is heavily damaged and was unproductive. A fringe of secondary woodland and open scrub on the northeast coast at Playa Bibijagua was moderately diverse, but contributed no species not found more frequently at El Abra. West of Nueva Gerona along the north coast, the land is almost entirely farmed or cultivated, and was extremely depauperate in butterflies.

Eastern Group

A second species-rich area of newer and more open secondary forest and scrub lies southeast of La Reforma (Fig. 5); to the east, patches of well-preserved forest merge with a coastal mangrove belt. This area, and cleared hillside west of the town, and areas south to the edge of the Ciénaga de Lanier have contributed most records from the east of the island. Sampling also was carried out in uniformly species-poor agricultural land and citrus plantations, at intervals along the road from La Fé to Cayo Piedra.

Western Group

Sampling was performed along road margins from Nueva Gerona to Playa Rojas (Colony), passing through the Sierra de La Cañada, near La Demajagua,



Fig. 2–5.—2. Edge of recent secondary forest at El Abra, with forested hill of the Sierra de Casas. 3. Low vegetation and exposed limestone in the Ciénaga de Lanier near Cayo Piedra, late in the dry season (March). Such areas are extensively flooded during the wet season. 4. Marble quarrying and agriculture in the Sierra de Casas, near El Abra. Note residual forest on hill slopes to the left. 5. Open secondary forest near La Reforma.

and from La Fé to the nature preserve of Los Monos, at the edge of the Ciénaga and marking the northern fringe of the forest covering the south of the island. A protected white-sand area near Río los Indios, including original pinewoods, still supports *Eumaeus atala*, but *Oarisma nanus* was last seen there in 1976. Western areas are generally heavily cultivated and species-poor, including the plantations of pine that now largely replace the original stands of the Sierra de La Cañada and elsewhere. The species list compiled for the western region was the most limited; no areas approaching the diversity of El Abra and La Reforma were found.

Southern Group

Localities visited in the low, densely forested southern part of the island generally followed the few established roads and tracks (Fig. 1). Although in places the forest is secondary growth produced by felling for charcoal burning, near present or former small settlements, much of this forest is undisturbed. Localities surveyed within the forest include: from Cayo Piedra to the meteorological station at Punta del Este and Cerro Caudal, Rincón de Guanál, Carapachibey, from Cocodrilo to Hato Milián (Fig. 6), and Pedernales (Fig. 7), approaching the tip of the southwestern peninsula. Mangrove and coastal scrub were sampled near Punta del Este, and cleared areas, on the track towards Playa Blanca, at Rincón de Guanál, Hato Milián, and Lugo (near Punta de Pedernales). The distribution of species across the southern zone was not uniform: the forest in the extreme east, around Punta del Este, was unaccountably poor during our visits (other than the slightly elevated area of Cerro Caudal), and species richness increased towards the west, with greatest diversity from Carapachibey to Hato Milián and Punta de Pedernales.

We did not attempt to survey the Ciénaga de Lanier, which in the wet season is extensively flooded and includes expanses of sawgrass and in the dry season (Fig. 3) contains wide areas of exposed limestone supporting few flowers as nectar sources. Brief excursions into the swamp yielded few butterflies, and all of species found more plentifully elsewhere.

RESULTS AND DISCUSSION

The Species List in Holland (1916)

Before discussing the results of recent surveys (Table 1), several points arising from the account by Holland (1916) need brief commentary. These concern changes in nomenclature and corrections resulting from our examination of Holland's material in Carnegie Museum. It should be borne in mind that at the time of Holland's work distributional information on Antillean butterflies was often incomplete, and taxonomic arrangement of some groups has been revised subsequently.

A few taxa cited by Holland were misidentified: *Lucinia sida* was listed as *L. cadma*, a Jamaican endemic; and his "*Anartia lytrea*" is actually the Cuban endemic *A. chrysopelea*. Holland's specimens of *Junonia coenia genoveva* proved to be *J. evarete* (sensu Turner and Parnell, 1985). The hairstreak specimen listed by Holland as "*Thecla favonius*" is instead the Cuban subspecies of *Electrostrymon angelia*. Holland regarded Link's series of the common pierid *Eurema daira palmira* as *E. elathea*, a similar species occurring in the far east of Cuba. Another *Eurema* that requires comment is Holland's "albino female" of "*Terias citrina*";



Fig. 6, 7.—6. Edge of the semideciduous limestone forest on the southwestern peninsula, from the cleared Guardia Forestal settlement at Hato Milián. 7. Low, exposed coastal limestone reef on the southwestern peninsula, near Punta de Pedernales. The coastal scrub vegetation merges with the semideciduous forest, often via a mangrove belt (Fig. 1).

we reidentified this specimen as *E. messalina*, a species now widespread on the Isle of Pines. Early records of another pierid group, the genus *Phoebis*, also call for clarification. The four specimens in Link's collection listed by Holland as "*Catopsilia agarithe fornax*" are correctly of the Cuban endemic *Phoebis argante fornax*. The collection studied by Holland does not include *P. agarithe antillia*, now widespread on the Isle of Pines, while *P. argante* has not been found there subsequently. Holland's "*Catopsilia editha*" instead represents *Aphrissa neleis*, now locally common on the Isle of Pines, and his "*Catopsilia neleis*" actually pertains to *Aphrissa statira*, a species more common than *A. neleis*. Two hesperiids described by Holland as new, supposedly endemic taxa require commentary: "*Telegonus geronae*" and "*Amblyscirtes insulae-pinorum*" were later recognized

(Alayo and Hernández, 1987) as synonyms, respectively, of *Astraptes cassander* and *Euphytes c. cornelius*, also present on the main island. Lastly, *Eurema priddy* was described from Haiti (Lathy, 1898) and a subspecies *forbesi* was described later from Isle of Pines specimens (Klots, 1929). We regard *E. priddy forbesi* as a synonym of *E. lucina*; the latter was included in Holland's list and still occurs on the island.

The Fauna and Seasonality

In all, 111 butterfly species have been recorded to date on the Isle of Pines, of which we have seen 106 in the field (Table 1). In summary, to Holland's list of 65 species may be added early specimens of *Libytheana motya*, *Eunica monima*, and *Nesiostrymon celida* that we have found in museum collections, bringing the total for species recorded in the first two decades of the century to 68 (Table 1). Fieldwork in 1975–1976, which included the southern forest for the first time, added 25 species to the island's list, and 18 more have been added from 1993 to 1995.

Two of our recent visits took place in the wet season (in July and August) and two others occurred late in the dry season (March). As in other Antillean islands, regular recording is essential to provide a picture of the seasonality or phenology of Isle of Pines butterflies. Nonetheless, the expected overall reduction in numbers of adult butterflies (individuals on the wing) in the dry season is marked. Much of our summer visit in 1993 was spent in a broad survey that included species-poor northern localities and yielded only 54 species records. A more representative tally of 87 species was recorded in summer 1995, while the dry season visits yielded 62 and 55 species, respectively.

Conditions in all localities visited in March 1995 were extremely parched after prolonged drought; numbers of butterflies were generally low. However, on the southwestern peninsula the most frequent skipper was *Proteides maysi*, generally considered rare, but outnumbering "common" species such as *Pyrgus oileus* and *Urbanus dorantes*. Such transient anomalies exemplify the unbalanced view of a fauna that can result from a brief period of fieldwork. At this time, however, flowers of *Eupatorium odoratum*, *Bidens alba*, *Stachytarpheta jamaicensis*, and species of *Solanum* were newly opening, and while most specimens of some species (e.g., *Marpesia eleucha*, *Anartia jatrophae*, *Siproeta stelenes*, *Dryas iulia*, *Strymon columella*, *Heraclides andraemon*, *Polygonus leo*, *Urbanus dorantes*, *U. proteus*, and *Wallengrenia misera*) were very worn, others (e.g., *Doxocopa laure*, *Heliconius charitonia*, *Appias drusilla*, *Phoebis sennae*, *Protesilaus celadon*, *Proteides mercurius*, *P. maysi*, *Achlyodes mithridates*, and *Ephyriades brunnea*) were uniformly fresh, suggesting that the onset of emergence of some species is synchronized with availability of plentiful nectar prior to the spring rains.

Most species were recorded in varying numbers during both wet and dry seasons. Most are evidently at least bivoltine, some continuously brooded. Some taxa were recorded on only one visit; e.g., *Anetia briarea* and *Aguna claxon* were seen only in March 1994, and *Astraptes talus* was locally abundant in the east in August 1994 but absent from the same locality in March 1995. Analysis of voltinism must await data on localities worked at regular intervals. Moreover, marked fluctuations in timing of emergence from year to year is well known in Antillean butterfly faunas (Schwartz, 1989; Smith et al. 1994b). Where voltinism is well documented on the main island, as for *E. celadon*, the spring emergence is

matched on the Isle of Pines; an infrequent, second emergence documented on the main island has yet to be recorded on the Isle of Pines.

Regional Distribution

Despite the incompleteness of data on voltinism, cumulative records from the past 20 years provide a picture of the regional distribution of the 106 recorded species. In all, 91 species have been found south of the Ciénaga de Lanier, and 96 from pooled localities north of this ecological divide. During 1993–1995, 81 species were recorded from northern and eastern localities combined whereas only 32 species were documented for western localities. The richness of the south is indicated by the fact that this zone represents only 33% of the island's area and that it received only one-third of our field time during recent visits. Furthermore, sampling is more difficult in the southern terrain, compounding the likelihood of overlooking very local species or missing species not in flight during our visits.

The richness of the little-disturbed southern area is not surprising; more remarkable was the discovery that the region north of the Ciénaga supports a butterfly fauna comparable with that of the southern forest. Although the land area of the north is almost twice that of the south, its long history of habitation, farming and cultivation, recent extensive conifer planting, citrus silviculture, and inundation by damming of rivers might be expected to have reduced species diversity. However, we suggest that this northern diversity is extremely precarious and markedly concentrated in a few very small areas: El Abra south of Nueva Gerona, near La Reforma in the east; and to a lesser degree in pockets of secondary woodland at Playa Bibijagua. Each of these sites is very vulnerable to land clearance; less than one mile from the El Abra locality, a component hill of the Sierra de Casas has been half-removed by marble quarrying (Fig. 4), and another entirely leveled since 1976. Elsewhere, we have seen encroachment into these unprotected areas between July 1993 and March 1995, and were they to be destroyed, we believe that species diversity at present collectively credited to the north of the island would decline precipitously to the low level now seen in the highly disturbed localities characterizing much of the island above the Ciénaga de Lanier.

It seems likely that these isolated, species-rich enclaves support relict faunas, surviving from the time when the northern hill ranges were covered in primary deciduous and pine forests, presumably including other varied ecosystems in the northern lowlands. If so, it is remarkable that such relatively small areas, now by no means undisturbed, should have preserved their present level of diversity. It is possible that the fauna of the southern zone has acted as a reservoir in maintaining this level, since the narrow Ciénaga de Lanier is unlikely to offer any barrier to movement of most butterflies in either direction.

The numbers of species recorded north and south of the Ciénaga are similar, but to what extent is the fauna of the island homogeneous? At present, 18 species are known from the north but not the south, and seven conversely. In the former group, *Eumaeus atala* and *Oarisma nanus* occur only in lateritic pineland, not present in the south, and *Burca braco* may be restricted to open, dry western sandy areas. *Anetia briarea*, *Calisto sibylla*, *Marpesia chiron*, and *Heraclides aristodemus* are generally upland species in Cuba, while *Historis acheronta* is more frequent in forest more moist than that of the south. *Anartia chrysopelea*, a butterfly of the forest edge, was common and widespread in 1975–1976 but has not been seen on the island subsequently. The southern zone does not include the

open land in which *Battus devilliers* is most frequent on the main island, or the disturbed land most suited to *Eurema lucina*. Southern localities apparently suitable for *Hamadryas amphicloë*, *Lucinia sida*, *Eurema boisduvaliana*, *Astraptes cassander*, *A. talus*, *Gesta gesta*, and *Panoquina corrupta* are present, and most of these species, so far unrecorded from the south, may prove to occur there.

Of the species known only south of the Ciénaga, ecological ties are even less obvious. *Danaus eresimus* was found only in the southern edge of the Ciénaga, but probably occurs along both margins of this swamp. *Eurema amelia* was collected by Link at Nueva Gerona and Los Indios and recorded from the southern forest in 1975–1976, but since then has not been seen on the island. *Brephidium exilis* is restricted to salt marshes and may also occur in the north; a similar situation pertains to the mainly coastal *Panoquina panoquinoides*. *Kricogonia lyside*, a strong dispersalist, is unlikely to be limited to the southern forest when populations are large. Both *Strymon limenia* and *Parachoranthus magdalia* are ecologically tolerant; each has been found only once in the south and may well have been overlooked in the north. The Central American *Aguna claxon*, however, probably a recent colonist, also has become established in the dry forest of the Guanahacabibes Peninsula (Hernández et al., 1994), ecologically similar to that of the south of the Isle of Pines.

Faunal Size and Comparisons

In considering the butterflies recorded from the Isle of Pines, while a single species number provides an index to overall diversity, its significance needs to be qualified. While the size of an island fauna may reflect a balance between colonization and extinction (Munroe, 1948, 1953; MacArthur and Wilson, 1963, 1967), these processes are seldom recognizable as discrete events within incompletely documented faunas (Smith et al., 1994a), particularly where phenology is little known. As for any Antillean butterfly faunal list, the present species total of 111 for the Isle of Pines is provisional, likely to increase with future work. In August 1994, six species were newly recorded from the island: *Historis acheronta*, *Eurema proterpia*, *Aguna claxon*, *Astraptes talus*, *Gesta gesta*, and *Parachoranthus magdalia*. While *Phoebis argante*, *Ephyriades arcas*, and *Lerodea eufala* have not been seen since the Carnegie expeditions, and the early record of *Nesiostrymon celida* has yet to be repeated, it cannot be assumed that any of these taxa is now extinct. For example, *Strymon martialis* was found in August 1994, the first record since May 1912.

The present species list for the Isle of Pines, albeit provisional, provides a basis for comparing biodiversity with other subsets of the Cuban fauna and for consideration of the origins of the fauna. From the ecological standpoint, the island's fauna may be compared with that of the Guanahacabibes Peninsula, which recently has been studied intensively and tabulated (Hernández et al., 1994). In all, 123 species have been recorded from the two areas combined, of which 86 (70%) are common to both. Sixteen species are known from Guanahacabibes but not from the Isle of Pines, while 21 are recorded on the Isle of Pines but not on the mainland peninsula. The area of Guanahacabibes Park (780 km²) is almost identical to that of the southern forest of the Isle of Pines (ca. 0.7% of the total land area of Cuba), and each includes well-preserved, semideciduous limestone forest with coastal limits (Samek, 1973) and is located adjacent to long-cultivated land. Both areas have suffered minimal human alterations and currently share some

degree of protection. Their faunas, however, while approximately similar in size, are distinctive. The Guanahacabibes forest has been surveyed more intensively, and at present 101 butterfly species have been recorded there. Some 19 species are known from Guanahacabibes that have not been recorded from the southern forest of the Isle of Pines, and the same number conversely. Each of the two regions supports about 40 Cuban specific or subspecific endemics, or over half the total for Cuba. Among the major families, the proportional representation of danaiids, nymphalids, and papilionids of Cuba as a whole is almost identical in the two regions. The higher species count for the Isle of Pines largely reflects diversity of lycaenids and hesperiids; the insular fauna includes 70% of the Cuban total for each family, a somewhat better representation than at present known from Guanahacabibes.

A noteworthy aspect of the butterfly fauna of the Isle of Pines is its lack of obvious evolutionary divergence from that of the main island. Throughout the West Indies, inter-island gaps narrower than the Gulf of Batabanó frequently have provided sufficient isolation for divergence (Smith et al., 1994a, 1994b). Two hesperiids described by Holland (1916) as new were later synonymized with two other taxa (Table 1). Alayo and Hernández (1987) suggested that another skipper, *Pyrrhocalles antiqua*, may differ subspecifically on the Isle of Pines from the main island subspecies *orientis*, but enlarged series now available show no divergence. Indeed, examination of series of all butterfly taxa from the Isle of Pines and Cuba as a whole demonstrates the phenotypic homogeneity of these often widely separated populations. We believe that the reason for this lies in the geologic history of the Isle of Pines and its pattern of colonization.

Origins of the Fauna

We suggest that the lack of divergence of Isle of Pines butterfly populations from those in Cuba stems from the hydrographic profile and history of the Gulf of Batabanó. The unnavigability of this stretch of water was recognized by mariners, and on early maps the Isle of Pines was sometimes represented as a peninsula of the south coast of Cuba (Jiménez, 1976). At its deepest, the gulf is only 10 m, and much is as shallow as 2–3 m (Anonymous, 1991). Lowering of sea water would have provided substantial land links with Cuba many times during the Pleistocene glaciation cycles, while the ancient high land of the Sierras, at least, would have remained emergent and accessible to dispersal from the main island during interglacial periods. During the last full glacial period (ca. 20,000 YBP), when the Florida peninsula was twice its present area (Webb, 1990), the Isle of Pines and Cuba would have been substantially linked (Webb, personal communication), and overland exchange of biotas would have been possible, whether or not the hills acted as refugia for earlier colonists. Also, air-borne dispersal presumably continues to contribute to colonization, but the means of colonization used by each taxon in the present fauna remains unknown. However, it may be inferred that the two *Calisto* of the Isle of Pines, members of a sedentary genus showing no ability to disperse over water throughout its range (Smith et al, 1994a), arrived overland. Whatever routes were followed in establishing the present butterfly fauna, the history of colonization seems to have been insufficiently long, or isolation sufficiently effective, for obvious evolutionary divergence to have made an imprint on the island's butterflies.

Genetic Comparisons

Wing pattern is the character most widely used in descriptions of island butterfly subspecies. However, morphological or phenotypic similarity may mask divergence at the genetic level. Davies (1995) analyzed populations of *Anartia jatrophae*, *Dryas iulia*, and *Heliconius charitonia* on the Isle of Pines and on the main island of Cuba using enzyme electrophoresis. Each of these species has evolved island races in the West Indies, most notably *Dryas iulia* with 12 named subspecies across the islands (Smith et al., 1994a). The results of the survey indicate, however, that extremely little genetic differentiation for populations of sampled taxa between Cuba and the Isle of Pines. This is consistent with earlier phenotypic assessment which grouped Isle of Pines populations with the Cuban races: *A. j. guantanamo*, *D. i. nudeola*, and *H. c. ramsdeni*. Despite the overall genetic similarity for each of these three species, samples from the Isle of Pines were more similar to samples from nearby western Cuba than to those from eastern Cuba. This suggests that, for these butterflies at least, a short water barrier has been a less significant factor in permitting genetic change than overall distance. The observed close genetic similarity may reflect significant gene flow between western Cuba and the Isle of Pines through dispersal, relatively recent colonization, and/or minimal genetic divergence between originally contiguous populations that became separated after the loss of the last Pleistocene land link.

In introducing the Isle of Pines butterflies collected for Carnegie Museum, Holland (1916) noted that they "...seem scarcely to adequately represent what must be a rather rich fauna, if we are justified in drawing conclusions from what we know of the wealth of insect-life which is found in Cuba," and surmised that his list might lay the foundation for a more complete account in the future. We conclude that his forecast was correct, with two-thirds of the total list of Cuba's butterfly species and with a good representation of endemic taxa now recorded from this small island. We, in turn, forecast that phenological and genetic studies will prove critical to the enhancement of our understanding of the island's butterflies. Moreover, continued monitoring is needed to document the future of extremely localized and equally vulnerable taxa in the north. Whether or not the latter survive, conservation of the remarkably preserved southern forest will maintain much of the richness of the butterfly fauna of the Isle of Pines.

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RODENTS AND LAGOMORPHS (MAMMALIA) FROM THE
LATE CLARENDONIAN (MIOCENE) ASH HOLLOW FORMATION,
BROWN COUNTY, NEBRASKAWILLIAM W. KORTH¹

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ABSTRACT

Twenty-five species of rodents and lagomorphs are recognized from Pratt Quarry, Brown County, Nebraska. Of these, four are new: the beaver *Dipoides tanneri*, the heteromyid *Cupidininus prattensis*, the cricetid *Antecalomys phthanus* (also new genus), and the leporid *Pronotolagus whitei*.

The rodent and lagomorph fauna from Pratt Quarry is clearly transitional between Clarendonian and Hemphillian because it contains the first record of four typically Hemphillian taxa (*Dipoides*, sigmodontine cricetids, *Hypolagus vetus*, leporine leporids), and the last record of eight Clarendonian or earlier taxa (*Protospermophilus*, *Petauristodon*, *Eucastor*, *Phelosacomys*, *Mioheteromys*, *Copemys*, *Tregomys*, and *Hesperolagomys*). This combination of first and last occurrences verifies a latest Clarendonian age for the fauna and the Merritt Dam Member of the Ash Hollow Formation.

KEY WORDS: Clarendonian, rodent, lagomorph, systematics

INTRODUCTION

Pratt Quarry was discovered in the 1930s and fossils were collected intermittently over the next 40 years by parties from the Frick Laboratory of the American Museum of Natural History (Skinner and Johnson, 1984). During these expeditions, 179 fossil mammal specimens were recovered, predominantly of larger mammals. The only rodents recovered were the larger beavers and some mylagaulid material. Screening for small vertebrates at Pratt Quarry was undertaken first in 1989 by a field party from the University of Nebraska State Museum. Again, in 1994, collection of microvertebrates was undertaken by the Rochester Institute of Vertebrate Paleontology, sponsored by the University of Nebraska. The screening operations have yielded several hundred identifiable specimens of small mammals which are the basis of this study. Previously, only the moles (Talpidae) from Pratt Quarry had been studied (Rudnick, 1992).

Pratt Quarry is in the Merritt Dam member of the Ash Hollow Formation (Skinner and Johnson, 1984). The age of the Merritt Dam Member has been established as late Clarendonian based on preliminary faunal analysis (Voorhies, 1990a). The legal location and a stratigraphic section of the quarry were presented by Skinner and Johnson (1984:310, fig. 26, 37). The quarry is a stream channel deposit that cuts into the underlying strata of the Cap Rock member of the Ash Hollow Formation and the Burge and Devil's Gulch members of the Valentine Formation.

There are four fossiliferous horizons at Pratt Quarry: 1) the base of the channel cut, 2) approximately 5 m above the base of the channel, 3) approximately 10 m above the channel base, and 4) a thin layer of diatomite at the top of the section approximately 20 m above the base of the channel. The fossils from the 5- and

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10-m horizons came from lenses of clay-ball conglomerates discontinuously exposed across the section. Among the clasts in the basal conglomerate are numerous bone fragments that are much more heavily worn than the majority of the fossils and appear to be reworked from the underlying strata. This difference in wear suggests that some of the faunal elements from the quarry may be reworked from these older layers. However, nearly all species identified here are from all levels. The only difference in occurrence of species throughout the section appears to be controlled by the dynamics of the depositing stream. The larger rodents (beavers, mylagaulids) are predominantly from the base of the section and are more poorly represented in the higher levels, whereas the smaller rodents (cricetids, heteromyids, sciurids) are most common from the horizon 10 m above the base of the channel. There is no definite proof that suggests any of the species of rodents or lagomorphs cited below are from horizons lower than the Merritt Dam member.

The rodents and lagomorphs from Pratt Quarry are significant because of the paucity of micromammals from the Clarendonian of the Great Plains. The only other micromammalian faunas of Clarendonian age from the Plains are the Mission fauna from South Dakota (Green, 1971) and the WaKeeney Fauna from Kansas (Wilson, 1968). Both of these latter faunas cannot be placed with confidence within the Clarendonian as early or later, and the Mission fauna of micromammals consists of fewer than 20 specimens of isolated teeth. The lithostratigraphic sequence that includes Pratt Quarry is well exposed and its relation to other layers in the local stratigraphic section is clearly defined. This relationship allows for a direct comparison of the fossils from Pratt Quarry to those from the subjacent strata and enhances the biostratigraphic value of the fauna.

Dental terminology used below for rodents follows that of Wood and Wilson (1936) with specialized terminology for castorids as defined by Stirton (1935). Lagomorph dental terminology used is that of White (1987, 1991). Abbreviations for institutions: AMNH, American Museum of Natural History; FAM, Frick Collections, AMNH; KU, University of Kansas Museum of Natural History; UNSM, University of Nebraska State Museum; UOMNH, University of Oregon Museum of Natural History; USNM, National Museum of Natural History, Smithsonian Institution. Abbreviations for dental measurements and statistical values are given in Table 1. Measurements in tables are given in millimeters.

SYSTEMATIC PALEONTOLOGY

Order Rodentia Bowdich, 1821

Family Mylagaulidae Cope, 1881

Mylagaulus Cope, 1881

Mylagaulus monodon Cope, 1881

(Fig. 1, Table 1)

Referred Specimens.—UNSM 101710–101717, isolated P₄; UNSM 101735, dP₄; UNSM 101718–101724, 101796, isolated P₄; UNSM 101729, fragmentary mandible with portion of lower incisor; UNSM 101725, proximal end of ulna; UNSM 101726, humerus; UNSM 101727, 101728, femora; UNSM 101732, ungual phalanx; UNSM 101797, astragalus; UNSM 101733, 101734, isolated incisors; UNSM 101736–101742, isolated molars.

Description.—The maximum length and width of both the upper and lower premolars are approximately at the level of the center of the tooth viewed laterally (half the maximum height of the tooth). In occlusal outline both premolars are elongated ovals. The occlusal pattern changes from fewer fossettes (-ids) in unworn specimens, to a greater number in moderately worn specimens. Upper

Table 1.—*Dental measurements of premolars of Mylagaulus monodon from Pratt Quarry. Abbreviations of dental dimensions used in all later tables: a-p, anteroposterior length; tr, maximum transverse width; tra, anterior transverse width (protoloph of upper cheek teeth, metalophid of lower cheek teeth); trp, posterior transverse width (metaloph of upper cheek teeth, hypolophid of lower cheek teeth). Statistical abbreviations: n, number of specimens; M, mean; OR, range of size; s, standard deviation; CV, coefficient of variation. Crown height measured only on unworn or little worn specimens. Measurements in mm.*

		n	M	OR	s	CV
P ₄	occlusal a-p	8	10.03	8.10–12.30	1.70	16.9
	occlusal tr	8	5.24	4.45–6.85	0.72	13.7
	maximum a-p	8	11.04	9.80–12.30	1.02	9.2
	maximum tr	8	5.38	4.80–6.85	0.63	11.8
	crown height	5	15.94	14.60–17.80	1.33	8.3
P ¹	occlusal a-p	6	8.72	7.20–10.95	1.46	16.7
	occlusal tr	6	5.62	4.45–6.40	0.70	12.4
	maximum a-p	6	9.56	8.15–10.95	1.01	10.6
	maximum tr	6	5.82	4.90–6.40	0.59	10.1
	crown height	3	13.53	11.30–16.30	2.54	18.8

premolars are concave on the lingual side for their entire height, whereas lower premolars are essentially straight-sided throughout their entire crown height.

In moderate wear, upper premolars have eight fossettes. All fossettes are narrow and anteroposteriorly oriented. There are three fossettes along the posterior margin (one lingual, one central, one buccal). A small fossette is near the center of the buccal margin of the tooth. Anteriorly there are three major fossettes arranged similarly to the posterior fossettes, and an additional, smaller fossette near the center of the anterior margin of the tooth. In earlier stages of wear, these eight fossettes are commonly fused to one another forming “star-like” fossettes. On an unerupted P¹ (UNSM 101721), there are only four recognizable fossettes: the central posterior fossette is fused with the central buccal fossette, the anterior and posterior lingual fossettes are fused, and the small central anterior fossette is fused with the main central anterior fossette in a “forked” shape. In the specimens showing little wear the anterior central fossette is always forked and the other fossettes are randomly fused, eventually to be separated into seven fossettes in later wear. In the most heavily worn specimens the fossettes are all nearly straight and anteroposteriorly oriented. Each fossette is distinct and never fused with another.

On the buccal sides of the lower premolars is a shallow groove that runs the entire height of the tooth. In early stages of wear there are as few as six fossettids on the occlusal surface: three along the posterior margin of the tooth, a single reentrant valley from the lateral groove on the tooth, a central anterior fossettoid that is anteriorly forked, and a small fossettoid on the anterior half of the tooth along the lingual margin. Commonly, there is a minute, circular accessory fossettoid which occurs at different places on the tooth. In later stages of wear, the forked anterior fossettoid splits into two and the number of fossettids is seven or eight. Like the upper premolars, in the very late stages of wear all the fossettids are nearly straight anteroposteriorly and do not fuse with one another.

Discussion.—The specimens referred here to *Mylagaulus monodon* are intermediate in size between the Hemphillian *Mylagaulus* from Oregon (Wilson, 1937) and Barstovian species identified as *M. cf. laevis* (Gazin, 1932; Storer, 1975; Voorhies, 1990b). The number of fossettes (-ids) on the premolars is also greater than those from the Barstovian.

In size, crown height, and complexity of the occlusal surface of the premolars, the Pratt Quarry species is comparable to both the holotype of *M. monodon* (Cope and Matthew, 1915:pl. CXIXc, fig. 11) and the sample of *Epigaulus minor* from Kansas (Hibbard and Philis, 1945). In the original description of *E. minor*, Hibbard and Philis (1945) suggested that this species might be conspecific with *M. monodon*. The difference between the genera *Mylagaulus* and *Epigaulus* is the presence of horn cores on the nasal bones of the latter. Because the holotype of

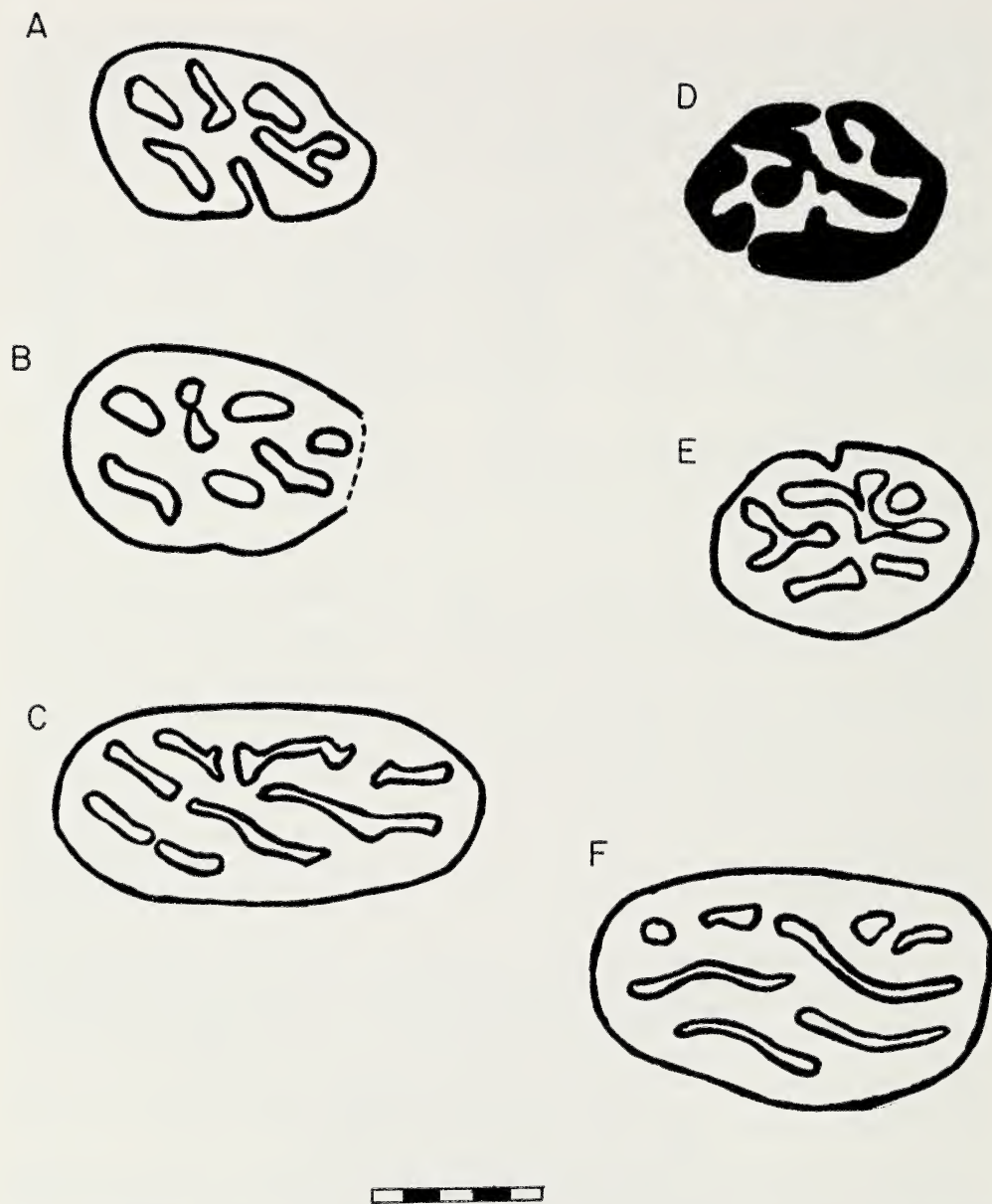


Fig. 1.—Premolars of *Mylagaulus monodon* from Pratt Quarry showing differing stages of wear: least worn (top) to late stages of wear (bottom). A–C, right P₄. A, UNSM 101713. B, UNSM 101714. C, UNSM 101715. D–F, left P₄. D, UNSM 101721 (unworn). E, UNSM 101718. F, 101723. Bar scale = 5 mm.

M. monodon does not include any skull material, the presence or absence of horn cores is unknown. If the holotype of *E. minor* were not a skull, this material might well have been referred to *Mylagaulus*. In fact, the type species of *Mylagaulus*, *M. sesquipedalis*, is known only from an isolated upper premolar. The presence or absence of horn cores is clearly not part of the definition of the genus.

Another difficulty with the synonymy of *M. monodon* and *E. minor* is the age of occurrence. *Epigaulus minor* is clearly from the Clarendonian WaKeeney fauna of Kansas. The holotype of *M. monodon* is most likely from the late Barstovian of southwestern Nebraska (Voorhies and Xue, 1983; Fiorillo, 1988; Voorhies, 1990a). Dentally, these species cannot be separated, therefore, the older name, *Mylogaulus monodon*, is used here.

The postcranials referred here to *M. monodon* are also identical in morphology and size to those of *E. minor* (Hibbard and Philis, 1945), and larger and more robust than those of the Barstovian *M. laevis* (Fagan, 1960).

Family Sciuridae Gray, 1821

Subfamily Sciurinae Gray, 1821

Tribe Marmotini Pocock, 1923

Protospermophilus Gazin, 1930

Protospermophilus sp., cf. *P. quatalensis* Gazin, 1930 (Fig. 2A)

Referred Specimen.—UNSM 101765, isolated M¹ or M².

Measurements.—a-p, 2.46 mm; tr, 2.72 mm.

Description and Discussion.—This specimen is separable from the remainder of the sciurines in the fauna by its greater relative length. In both species of *Spermophilus* and *Ammospermophilus* discussed below, the upper molars have a much greater transverse width than anteroposterior length. In UNSM 191765, the length is closer to the width, giving the tooth a much more squared appearance. There is a large cuspule at the lingual end of the posterior cingulum (= hypocone) characteristic of *P. quatalensis*. The only difference between UNSM 101765 and the M¹ of *P. quatalensis* from California (Black, 1963:pl. 13, fig. 4b) is the deep notch separating the protocone and hypocone which is lacking on the Pratt Quarry specimen. This notch on M¹ is a diagnostic character of *P. quatalensis*; however, the Nebraska specimen may well be an M². The M² of *P. quatalensis* does not have as pronounced a notch as the M¹.

Protospermophilus quatalensis has been reported only from the latest Barstovian and earliest Clarendonian of California (Gazin, 1930; Bryant, 1945). This occurrence of *Protospermophilus* extends the record of the genus to the late Clarendonian.

Spermophilus Cuvier, 1825

Spermophilus (*Otospermophilus*) Brandt, 1844

Spermophilus (*Otospermophilus*) sp.

(Fig. 2F–H, Table 2)

Referred Specimens.—UNSM 101590, 101799, isolated dP⁴; UNSM 101585–101589, 101591, 101746, 101765, isolated M¹ or M²; UNSM 101583, edentulous maxilla; UNSM 101580, 101584, 101766, 101767, isolated M₁ or M₂; UNSM 101578, 101581, isolated M₃; UNSM 101579, 101582, partial mandibles without cheek teeth.

Description.—The lower molars are brachydont and cusped, typical of the subgenus *Otospermophilus*. The lower premolar is not represented in the collection. The anterior molars are rhomboidal in occlusal outline, and wider than long. The first molar cannot be differentiated with certainty from M₂. The anterior width of the molars (metalophid) is less than the posterior half of the tooth. The metaconid, protoconid, and hypoconid are bulbous, showing little or no compression. The entoconid is reduced to a curve at the lingual end of the posterolophid. The lingual half of the tooth is shorter (anteroposteriorly) than the buccal half. There is a minute mesostylid present on all specimens. The trigonid basin is small and obliquely oriented, bounded anteriorly by a ridge running buccally from the apex of the metaconid (metalophid I), and bounded posteriorly by a short posterior arm of the protoconid. The trigonid basin is slightly open posteriorly because the posterior arm of the protoconid (metalophid II) is not continuous with the base of the metaconid. The ectolophid is weak, and on little-worn specimens a minute mesoconid is present.

The last lower molar is similar to M₁ and M₂ except it is elongated posteriorly and has a narrower posterior half. There is evidence of a small mesoconid and mesostylid on M₃.

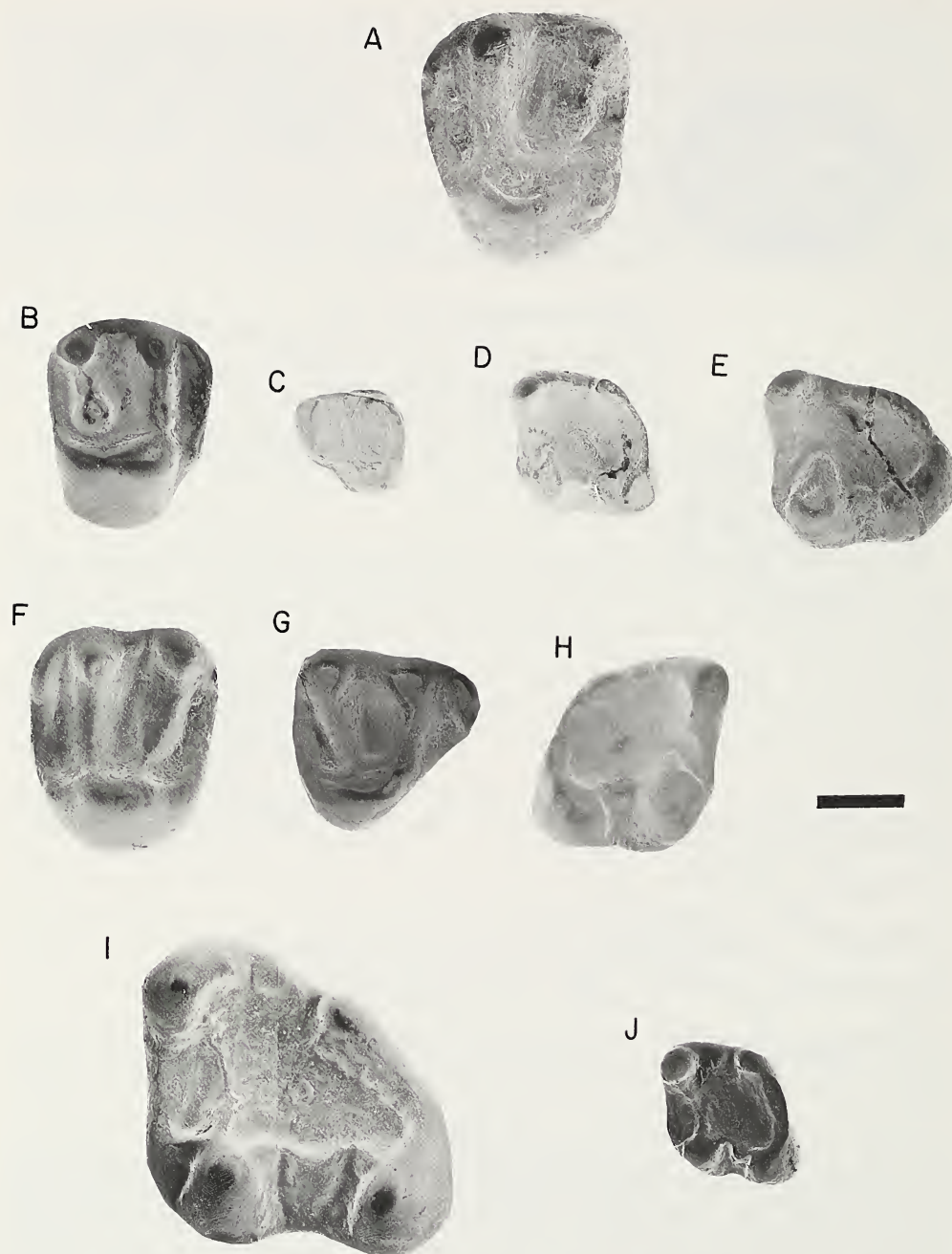


Fig. 2.—Scanning electron micrographs of cheek teeth of sciurids from Pratt Quarry. A, *Protospermophilus* sp., cf. *P. quatalensis*, left M¹ or M², UNSM 101765. B–E, *Ammospermophilus juturensis*. B, right M¹ or M², UNSM 101762. C, left P₄, UNSM 101755. D, left M₁ or M₂, UNSM 101758. E, left M₃, UNSM 101763. F–H, *Spermophilus* (*Otospermophilus*) sp. F, left M¹ or M², UNSM 101746. G, right dP₄, UNSM 101590. H, right M₁ or M₂, UNSM 101766. I, ?*Petauristodon* sp., left M₃, UNSM 101659. J, cf. *Sciurion* sp., left M₁ or M₂, UNSM 101769. Bar scale = 1 mm.

Table 2.—Dental measurements of *Spermophilus* (*Otospermophilus*) sp. from Pratt Quarry. Abbreviations as in Table 1. Measurements in mm.

UNSM No.	M ₁ or M ₂			M ₃			P ₄ -M ₃	dP ⁴		M ¹ or M ²	
	a-p	tra	trp	a-p	tra	trp		a-p	tr	a-p	tr
101578				—	2.12	—					
101580	1.89	1.92	2.15								
101581				2.90	2.72	2.41					
101584	1.99	2.10	2.13								
101579							8.75				
101766	1.96	2.23	2.09								
101585										2.01	2.42
101586										2.21	2.89
101587										2.45	2.98
101588										2.25	2.96
101589										2.00	2.67
101590								2.04	1.99		
101591										2.00	—
101799								2.02	1.88		

The mandible is generally slender, but more heavily built than in species of the subgenus *Spermophilus*. The masseteric scar is U-shaped. It ends anteriorly below the posterior roots of P₄. The dorsal margin of the diastema is shallow. The mental foramen is high on the side of the mandible, just below the margin of the diastema, approximately at its center. The lower incisor is elongated anteroposteriorly in cross section and strongly convex anteriorly. Enamel covers approximately half of the tooth on its lateral side.

The single dP⁴ (UNSM 101590) is triangular in occlusal outline. There is a large parastyle (= anterocone) on the anterobuccal corner of the tooth continuous with the anterior cingulum. It is crescentic in shape, and defines a wide valley between the anterior cingulum and the protoloph. Both the protoloph and metaloph converge on the protocone and are continuous with it. There is no evidence of a protoconule, but there are two minute wear facets on the metaloph indicating a doubled metaconule. The posterior cingulum runs the entire width of the tooth and ultimately runs into the apex of the protocone. On the posterior slope of the protocone is a small wear facet that indicates the presence of a small hypocone.

The upper molars are typical of other species of the subgenus *Otospermophilus*, and do not have the high degree of lophodonty as in species of *Spermophilus* (*Spermophilus*). The protoloph is complete from the paracone to the protocone with no protoconule. The metaloph ends lingually before meeting the protocone. There is a small metaconule at the lingual end of the metaloph. The anterior and posterior cingula are continuous from the buccal margin of the teeth and run nearly the entire width of the tooth. The anterior cingulum runs up the anterior slope of the protocone. The posterior cingulum is slightly longer than the anterior, and has a distinct bend at its lingual end as it fuses with the protocone. There is no evidence of a hypocone on any of the specimens. A small mesostyle is always present.

Discussion.—The cheek teeth of *Spermophilus* (*Otospermophilus*) sp. are proportioned as in other species of *Spermophilus* (wider than long), but do not have the amount of anteroposterior compression or lophodonty as in species of *S.* (*Spermophilus*). The only other species of *Spermophilus* from the Clarendonian are *S.* (*O.*) *matthewi* and *S.* (*Spermophilus*) sp. (= *Citellus* [*Citellus*] sp., Black, 1963). *Spermophilus* (*O.*) *matthewi* is markedly larger than *S.* (*O.*) sp. with a much more heavily built mandible (Black, 1963:202, pl. 18, fig. 2). The unnamed species of *S.* (*Spermophilus*), although similar in size to *S.* (*O.*) sp., is clearly distinguishable because of the greater compression and lophodonty of the lower cheek teeth that is characteristic of species of its subgenus (Black, 1963:pl. 22, fig.4).

The only other species of *S.* (*Otospermophilus*) similar in size to *S.* (*O.*) sp. are *S.* (*O.*) *argonautus* and *S.* (*O.*) *gidleyi*, both from the Hemphillian. *Spermo-*

philus (*O.*) *gidleyi* is diagnosed as having distinct ectostylids and posteriorly closed trigonids on the lower molars, whereas these features are lacking in *S. (O.)* sp. *Spermophilus* (*O.*) *argonautus* lacks the mesostylid and mesoconid on the lower molars that characterize *S. (O.)* sp. (Stirton and Goeriz, 1942:fig. 7e).

Spermophilus (*Otospermophilus*) sp. is surprisingly primitive with the possession of a mesoconid on the lower molars and only weakly lophate cheek teeth. Only the Barstovian species *S. (O.) primitivus* and *S. (O.) jerae* retain a mesoconid on the lower molars (Bryant, 1945; Black, 1963; Sutton and Korth, 1995). These species differ from *S. (O.)* sp. in size (*S. primitivus* larger, *S. jerae* smaller) and having better developed entoconids on the lower molars.

Ammospermophilus Merriam, 1892

Ammospermophilus junturensis (Shotwell and Russell, 1963)

(Fig. 2B–E, Table 3)

Citellus junturensis Shotwell and Russell, 1963.

Ammospermophilus? sp. Black, 1963.

Referred Specimens.—UNSM 101751, P³; UNSM 101592, 101752–101754, M¹ or M²; UNSM 101755, 101756, P₄; UNSM 101759, partial mandible with M₁–M₃; UNSM 101757, 101758, 101760, 101761, M₁ or M₂; UNSM 101762–101764, M₃.

Discussion.—Both the upper and lower dentitions of *Ammospermophilus junturensis* have been fully described by Shotwell and Russell (1963:44–46) and Black (1963:225–226). The specimens referred to this species from Pratt Quarry do not differ in size or morphology from the previously described material from Oregon. Specimens of *A. junturensis* from Pratt Quarry are easily separable from *Spermophilus* (*Otospermophilus*) in their smaller size. In addition, the lower molars are relatively wider with a more weakly developed ectolophid, and the upper molars have a larger, more distinct metaconule.

The fossil material from Pratt Quarry referred to *Ammospermophilus junturensis* is comparable in size and morphology to the topotypic material from Oregon (Black, 1963:226, pl. 22, fig. 6; Shotwell and Russell, 1963:table 6, fig. 38, 39). It differs from the only other Tertiary species of the genus, *A. fossilis*, in its slightly larger size (James, 1963:table 13).

Other than size, the most distinctive difference between the Tertiary species of *Ammospermophilus* and the Recent species is the morphology of anterior cingulum on the upper molars. In the Tertiary species it is less prominent and originates at the protocone, but does not have the 90° bend at its origin as do the molars of the Recent species (James, 1963).

Shotwell and Russell (1963) originally referred this species to *Citellus* (= *Spermophilus*). However, Black's (1963:225) arguments for assigning it to *Ammospermophilus* (based on the morphology of the lower cheek teeth) appear valid. Also, the similarity to the other Tertiary species, *A. fossilis*, which is known from cranial material, verifies the inclusion of *A. junturensis* in the genus *Ammospermophilus*.

Subfamily Petauristinae Miller, 1912

Petauristodon Engesser, 1979

? *Petauristodon* sp.

(Fig. 2I)

Referred Specimen.—UNSM 101659, left M₃.

Measurements.—a-p, 3.62 mm; tra, 3.59 mm; trp, 3.10 mm.

Table 3.—Dental measurements of *Ammospermophilus jurensis*. Abbreviations as in Table 1. Measurements of holotype taken from Black (1963:226). Measurements in mm.

UNSM No.	P ₄			M ₁			M ₂			M ₃			P ₃			M ¹ or M ²		
	a-p	tra	tp	a-p	tra	tp	a-p	tra	tp	a-p	tra	tp	a-p	tra	tp	a-p	tr	tr
101755	1.23	0.90	1.24															
101756	1.37	0.99	1.14															
101757							1.68	—	1.90									
101578				1.66	1.81	1.63												
101759				1.61	1.63	1.79	1.74	2.01	1.95									
101760							1.85	1.88	1.85									
101761				1.63	1.70	1.83				1.60	1.35	1.14				1.87	2.41	
101762										2.22	1.96	1.74				1.86	2.38	
101763										2.28	2.07	1.81				1.76	2.21	
101764													0.78	0.82		1.94	—	
101751																		
101592																		
101752																		
101753																		
101754																		
UOMNH No. (holotype)																		
F-5871	1.30	1.05	1.45	1.55	1.60	1.80	1.75	1.85	1.90	2.00	1.95	1.90						

Description and Discussion.—The isolated specimen referred here to *Petauristodon* varies from those of other species of the genus only in its larger size and less prominent crenulations in the talonid basin of the tooth (James, 1963; Lindsay, 1972; Engesser, 1979). If better represented, the Pratt Quarry specimen might well represent a new species.

Sciurion Skwara, 1986

cf. *Sciurion* sp.

(Fig. 2J)

Referred Specimen.—UNSM 101769, isolated left M_1 or M_2 .

Measurements.—a-p, 1.42 mm; tra, 1.50 mm; trp, 1.56 mm.

Description.—The single lower molar is smaller than all of the other sciurids from Pratt Quarry. It is rhomboid, with no evidence of the anteroposterior compression present in the molars of *Ammodontomys* and *Spermophilus*. There are faint enamel wrinkles in the talonid and trigonid basins. The metalophulid I runs from the apex of the metaconid along the anterior border of the tooth, ending in a distinct cuspule (= anterostylid) anterior and lingual to the protoconid. The trigonid basin is small and blocked posteriorly by a complete but low metalophulid II. The ectolophid is low and obliquely oriented with just a trace of a mesoconid. The posterolophid is continuous from the hypoconid to the entoconid. The entoconid is distinct and round, not compressed into the lingual end of the posterolophid as in the spermophiles. A small mesostylid is present posterior to the metaconid.

Discussion.—*Sciurion campestre* was named from the Hemingfordian of Saskatchewan (Skwara, 1986). The Pratt Quarry specimen differs from the type material in having a complete metalophulid II and less well-defined mesoconid. UNSM 101769 is also larger than the referred lower molar of *S. campestre* (Skwara, 1986:table 1). In size, UNSM 101769 is close to the European *Blackia*. *Blackia* was originally named for a small “flying squirrel” from the Miocene of Europe (Mein, 1970). UNSM 101769 differs from the described species of *Blackia* from Europe in having less pronounced wrinkling of the enamel on the cheek teeth, a complete metalophulid II, and a more distinct entoconid, mesostylid, and anterocoonid.

The only occurrence of *Blackia* in North America is based on several isolated teeth from the Hemingfordian of California (Hutchison and Lindsay, 1974) and the medial Barstovian of Nebraska (Voorhies, 1990b). The Pratt Quarry specimen is slightly smaller than the Barstovian lower molar from Nebraska (UNSM 85558) and has a complete metalophulid II (trigonid completely open in the Barstovian specimen) and a better developed entoconid, mesoconid, and mesostylid. The Pratt Quarry specimen differs from the Hemingfordian specimens in being larger and the features discussed by Skwara (1986) for *S. campestre*.

Family Castoridae Gray, 1821

Subfamily Castoroidinae Trouessart, 1880

Dipoides Jager, 1835

Dipoides tanneri, **new species**

(Fig. 3, 4, 5A–C, Table 4)

Type Specimen.—UNSM 101612, little worn P_4 .

Referred Specimens.—UNSM 101613–101620, P_4 ; UNSM 101621–101631, P_4 ; UNSM 101632–101653, 101795, 101798, FAM 64483–64487, isolated molars; UNSM 101654–101657, isolated incisors; UNSM 101730, distal humerus; UNSM 101731, proximal femur; FAM 64488, 64517, mandibles with P_4 – M_2 ; FAM 64482, complete skull with associated mandible and postcranial elements.

Diagnosis.—Similar in size to *D. stirtoni*; differs from all other species of the genus in the lower crown height of the cheek teeth (premolars develop roots in

very late stages of wear), upper premolars not attaining the S-pattern of the occlusal surface, and the lower premolar having a parastriid shorter than the mesostriid (parastriid not reaching the base of the tooth) as in *D. stirtoni*, and a small metafossettid retained until very late stages of wear (absent in other species).

Etymology.—Patronym for Lloyd Tanner, in recognition of his many years of work for the UNSM.

Description.—The nearly complete skull with heavily worn dentition (FAM 64482) lacks only parts of the zygomatic arches. Due to the advanced age of the individual, some of the cranial sutures are not distinguishable. Also, damage to the pterygoid and basicranial area has obscured the features and foramina of this area. In general shape, it is not as deep dorsoventrally as the skull of Recent *Castor*, and the rostrum is relatively longer. Wahlert (1972) fully described the skull of a Hemphillian *Dipoides* and noted only four differences in the cranial foramina between *Dipoides* and earlier *Eucastor* and *Monosaulax*: 1) posterior palatine foramina medial to M¹ in *Dipoides*, medial to the boundary of M¹ and M² in the other genera; 2) lateral margin of the infraorbital foramen forms part of the masseteric tubercle in *Dipoides* but continues into the tubercle in the other genera; 3) the sphenopalatine foramen is dorsal to the premolar in *Dipoides* and more posterior in the other genera; and 4) the ethmoid foramen is entirely within the frontal bone in *Dipoides* and passes through the frontal-orbitosphenoid suture in the other genera. Nearly complete skulls of *E. tortus* from the Valentine Formation of Nebraska (UNSM 85600) and *M. pansus* from New Mexico (FAM 64945) were compared with FAM 64482. All of the differences cited by Wahlert (1972) hold true for the skull of *D. tanneri* except for the morphology of the infraorbital foramen. In the skull of *D. tanneri* the foramen continues into the masseteric tubercle as in *Eucastor* and *Monosaulax*. Other than these differences, there is little distinction between the skulls of these three beavers.

One other feature of the cranial foramina of the Hemphillian *Dipoides* figured by Wahlert (1972: fig. 16) is the presence of three interorbital foramina posterior and ventral to the optic foramen. In the specimens of *Eucastor* and *Monosaulax* at hand, there are only two interorbital foramina. The skull of *D. tanneri* has three foramina as in the Hemphillian *Dipoides*. In size, the skull of *D. tanneri* is at least 50% larger than the skulls of the other two beavers.

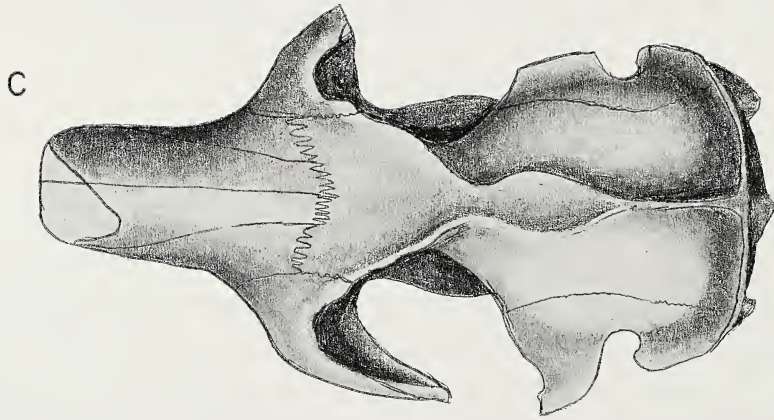
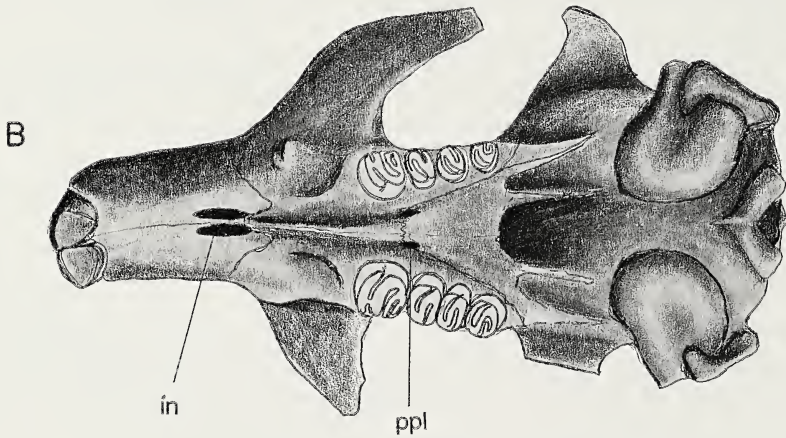
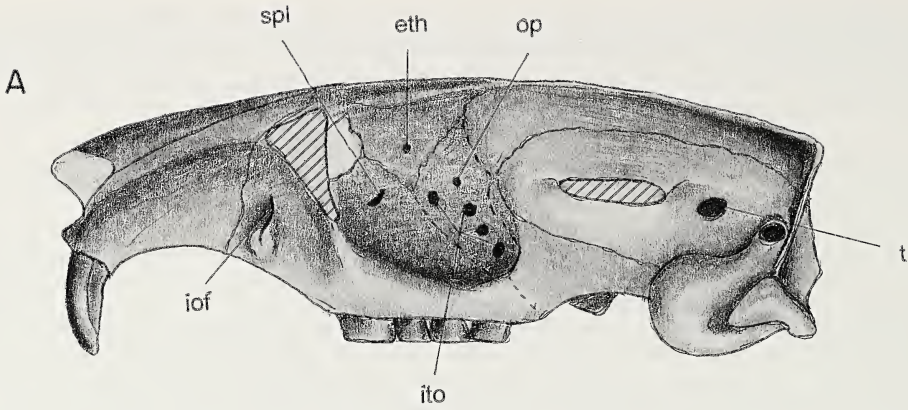
The molars of *D. tanneri* are hypsodont and rootless. The occlusal patterns of both the upper and lower molars quickly wear to the characteristic S-pattern of *Dipoides*. The flexi remain open and do not close to form fossettes (-ids) until the latest stages of wear.

M³ is distinct from the anterior molars. It does not taper towards the base of the crown. On the buccal side of the tooth, there is only one persistent stria, the mesostria. The parastria is much shorter, and a parafochette is formed after only moderate wear. The hypostria is continuous to the base of the crown and the hypoflexus is as in the anterior molars. In late stages of wear the parafochette is lost and the hypoflexus extends to the buccal margin of the tooth. On little-worn specimens there is a short metaetria. The metaflexus and mesoflexus isolate the metacone. After the metaetria has been worn away, the metacone remains isolated. The mesoflexus extends to the lingual margin of the tooth and is strongly concave posteriorly.

The premolars of *D. tanneri* develop roots only in the very late stages of wear. On the lower premolars, the buccal hypostriid and lingual mesostriid are continuous to the base of the crown, thus the hypoflexid and mesoflexid remain open throughout the life of the individual. The parastriid is slightly shorter than the mesostriid, ending only a few millimeters from the base of the crown. Because of the length of the parastriid, in very late stages of wear, the paraflexid closes lingually to form a parafochette. In occlusal view, the paraflexid, mesoflexid, and hypoflexid are all concave anteriorly and cross nearly the entire width of the tooth. The only variation is the presence of a small metafochette at the lingual end of the hypoflexid. This metafochette is present on all specimens except those with extreme wear.

The upper premolars are square in occlusal outline and the crown is strongly curved (concave buccally). On the lingual side of the tooth, the hypostria is continuous to the base of the crown. On the buccal side, the parastria and mesostria extend to within 2–4 mm of the base of the crown, but the metaetria extends less than half of the height of the crown toward the base of the crown. On the occlusal surface of the tooth, the hypoflexus and paraflexus meet on the buccal half of the tooth, being separated only by a thin enamel wall. The mesoflexus extends to the lingual border of the tooth. The metaflexus is only about half the tooth in length and closes off buccally after only moderate wear to form a small fossette. All of the flexi on P⁴ are concave posteriorly.

Discussion.—*Dipoides tanneri* is referable to this genus based on Stirton's (1935:440) diagnosis—high-crowned cheek teeth with striae (-ids) persistent to the base of the crowns. The skull of *D. tanneri* also has the distinctive features



of *Dipoides*, not present in *Eucastor* (posterior palatine foramina more anterior, ethmoid foramen entirely within the frontal bone, three interorbital foramina present posterior and ventral to the optic foramen, and the sphenopalatine foramen more anteriorly positioned).

Dipoides tanneri is clearly distinguishable from contemporaneous species of *Eucastor* because of these differences. The Clarendonian *Eucastor malheurensis* is similar to *D. tanneri* in crown height of the cheek teeth, but is much smaller than *D. tanneri* (Shotwell and Russell, 1963:table 8) and the striae (-ids) of the cheek teeth do not extend as far toward the bases of the crowns, thus forming fossettes (-ids) earlier in wear. Two species of *Eucastor* have been identified from the Clarendonian of the Great Plains, *E. dividerus* from Nebraska (Webb, 1969a) and *E. philisi* from Kansas (Wilson, 1968). Both of these species are similar in size to *D. tanneri* but do not have the persistent striae (-ids) of the cheek teeth of *D. tanneri* (Stirton, 1935:fig. 107–110; Wilson, 1968:text-fig. 15).

Dipoides tanneri differs from all other species of *Dipoides* in having lower-crowned cheek teeth, maintaining a metafossettid on P_4 until late stages of wear, having roots develop on the premolars in late stages of wear, having P^4 and M^3 not attain the S-pattern of the other molars, and having the parastrid shorter than the mesostrid on P_4 . All of these features are viewed as primitive and are shared with species of *Eucastor*.

Among species of *Dipoides*, *D. tanneri* most closely resembles *D. stirtoni* from the early Hemphillian of Oregon (Wilson, 1934). *Dipoides stirtoni*, like *D. tanneri* has a P_4 with a shorter parastrid than mesostrid. In all other species both of these striids extend to the base of the crown. Similarly, P^4 and M^3 of *D. stirtoni* do not wear to the occlusal S-pattern characteristic of *Dipoides*. *Dipoides tanneri* differs from *D. stirtoni* in having lower-crowned cheek teeth and developing roots on the premolars. The postcranial material assigned to *D. tanneri* differs from that of *D. stirtoni* only in being slightly smaller and less robust (Wilson, 1934:fig. 1).

Dipoides tanneri is the earliest occurrence of the genus. All other species of *Dipoides* are known only from the Hemphillian and Blancan (Korth, 1994:148). This earlier occurrence is compatible with the more primitive features of the dentition of *D. tanneri*.

Eucastor Leidy, 1858

Eucastor planus Stirton, 1935

(Fig. 5D–F, Table 5)

Referred Specimens.—UNSM 101594, partial mandible with incisor and P_4 – M_1 ; UNSM 101610, I_1 ; UNSM 101611, P_4 ; UNSM 101596, 101600, 101602, 101605, 101607–101609, 101611, 101658, M_1 or M_2 ; UNSM 101603, M_3 ; UNSM 101597, 101601, 101604, P^4 ; UNSM 101595, 101606, 101794, M^1 or M^2 ; UNSM 101598, 101599, M^3 .

Discussion.—The specimens referred here to *Eucastor planus* do not differ from the holotype from the Clarendonian of Oklahoma (Stirton, 1935) or other

←

Fig. 3.—Skull of *Dipoides tanneri*, FAM 64482. A, lateral view (zygoma removed). B, ventral view. C, dorsal view. Abbreviations of foramina: eth, ethmoid; iof, infraorbital; in, incisive; ito, interorbital; op, optic; pgl, postglenoid; ppl, posterior palatine; spl, sphenopalatine. Bar scale = 1 cm. Dashed lines indicate probable orientation of sutures.

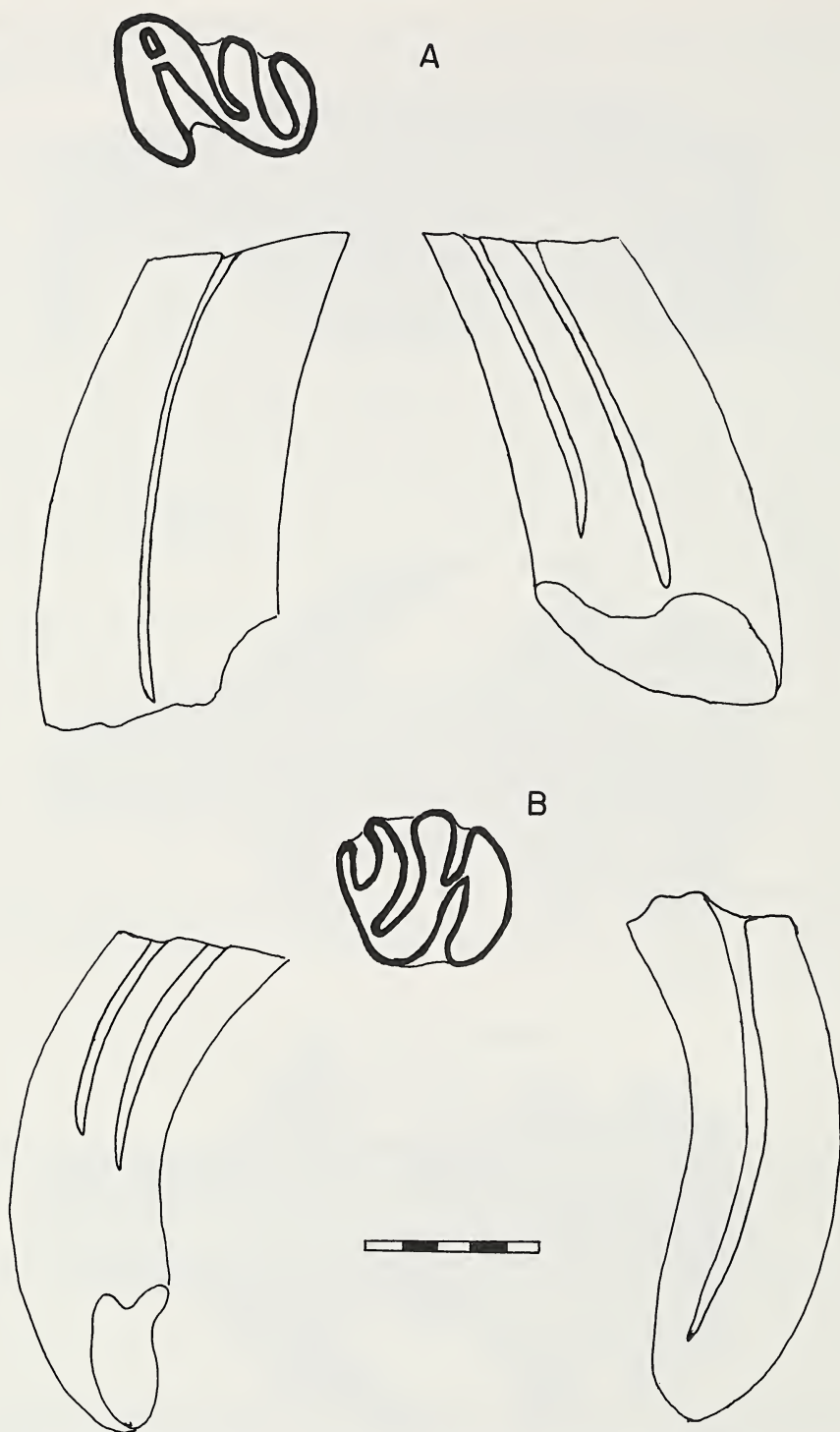


Fig. 4.—Unworn premolars of *Dipoides tanneri*. A, UNSM 101612, holotype, right P₄; occlusal view (above), buccal view (left), and lingual view (right). B, UNSM 101628, right P₄; occlusal view (above), buccal view (left), and lingual view (right). Bar scale = 5 mm.

Table 4.—Dental measurements of *Dipoides tanneri*. Abbreviations as in Table 1. Crown height measured only on unworn or little worn lower premolars. Measurements in mm.

Isolated premolars						
		<i>n</i>	M	OR	<i>s</i>	CV
P ₄	a-p	9	7.03	6.48–7.86	0.50	7.1
	tra	8	3.92	3.49–4.55	0.40	10.2
	trp	9	4.69	3.98–5.38	0.41	8.7
	crown height	5	14.20	13.40–15.60	0.85	6.0
P ⁴	a-p	11	4.47	3.92–5.01	0.29	6.5
	tr	11	5.22	4.70–5.59	0.29	5.6
Teeth in jaws						
FAM No.					FAM No.	
		64482	64488	64517	64482	(Left) (Right)
P ₄	a-p	6.28	6.10	6.39	P ⁴	a-p 6.10 6.31
	tra	4.41	4.10	4.40		tr 5.78 5.52
	trp	5.02	5.35	5.21		
M ₁	a-p	4.59	4.14	4.30	M ¹	a-p 3.90 3.81
	tr	4.80	5.09	4.88		tr 4.58 5.15
M ₂	a-p	3.40	3.82	4.25	M ²	a-p 3.87 3.80
	tr	4.39	5.01	4.64		tr 4.99 5.20
M ₃	a-p	4.76			M ³	a-p 4.49 4.25
	tr	4.00				tr 3.93 4.29
P ₄ –M ₃		19.79	20.10	19.88	P ⁴ –M ³	19.22 18.37

referred specimens of this species. This species is clearly separable from the other castorids from Pratt Quarry by its markedly smaller size, having higher-crowned cheek teeth than *Hystricops*, and having less well-developed striae (-ids) on the cheek teeth than in *Dipoides*. *Eucastor planus* has previously been identified in the early Clarendonian Burge and medial Clarendonian Minnechaduza faunas of northcentral Nebraska as well (Webb, 1969a; Voorhies, 1990a).

Subfamily uncertain

Hystricops Leidy, 1858

Hystricops venustus Leidy, 1858

(Fig. 6, Table 6)

Hystrix (Hystricops) venustus Leidy, 1858.

Hystrix venustus Leidy, 1869.

Erethizon venustus (Leidy) Hay, 1901.

Hystricops venustus Leidy: Stirton, 1935.

Referred Specimens.—UNSM 101660, P₄; UNSM 101661, 101662, 101775, M₁ or M₂; UNSM 101663, 101664, 101667, M₃; UNSM 101655, 101666, P⁴; UNSM 101668, 101669, upper molars; UNSM 101747, incisor fragment.

Description.—The cheek teeth are mesodont and strongly rooted, much lower crowned than the other castorids from Pratt Quarry, and clearly much larger in size (Table 6). One incisor fragment is preserved, UNSM 101747. It has a broad, gently convex, and smooth anterior surface.

The lower premolar is the largest of the cheek teeth. It has two roots. The only striids that are continuous to near the base of the crown are the hypostriid and the mesostriid. All others are very short, disappearing after only moderate wear. The mesoflexid is the longest of the flexids, extending nearly to the buccal edge of the tooth. The mesoflexid is gently curved anteriorly. The hypoflexid is much shorter, extending only about one-fourth the width of the tooth, posterior to the mesoflexid, in

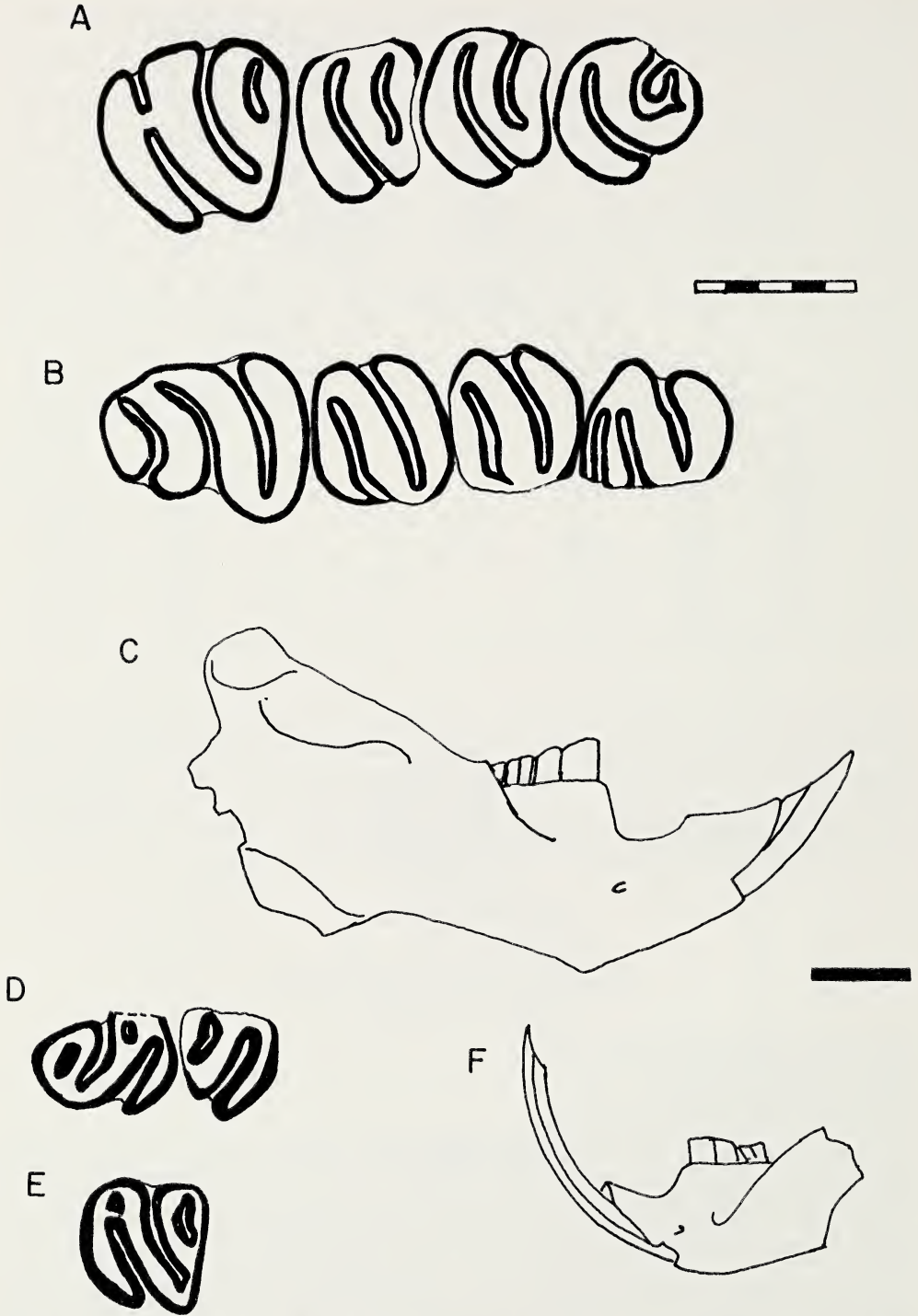


Fig. 5.—Cheek teeth and mandibles of castorids from Pratt Quarry. A–C, *Dipoides tanneri* FAM 64482. A, left P^4 – M^3 . B, right P^4 – M^3 . C, lateral view of mandible. D–F, *Eucastor planus*. D, UNSM 101594, left P^4 – M^1 . E, UNSM 101609, left P^4 . F, UNSM 101594, lateral view of mandible. Bar scale for teeth (above) = 5 mm. Bar scale for mandibles (below) = 1 cm.

Table 5.—Dental measurements of *Eucastor planus* from Pratt Quarry. Abbreviations as in Table 1. Measurements in mm.

		n	M	OR	s	CV
P ₄	a-p	2	4.40	4.27–4.52		
	tra	2	2.84	2.70–2.98		
	trp	2	3.47	3.34–3.60		
M ₁ or M ₂	a-p	8	3.10	2.72–3.51	0.32	10.2
	tr	8	3.74	3.02–4.09	0.42	11.6
M ₃	a-p	1	2.50			
	tr	1	2.89			
P ⁴	a-p	3	3.64	3.51–3.80	0.15	4.0
	tr	3	4.01	3.46–4.36	0.48	12.0
M ¹ or M ²	a-p	2	3.09	3.00–3.18		
	tr	2	3.60	3.50–3.60		
M ³	a-p	2	2.74	2.67–2.80		
	tr	2	2.63	2.41–2.85		

a posterolingual direction. On the anterior half of the tooth is a large, anteriorly concave parafoesettid. Irregularities of the enamel are preserved along its borders. Anterior to the parafoesettid is a much smaller foesettid that is straight and oriented transversely. Along the lingual border of the tooth between the mesoflexid and the parafoesettid is a short flexid that is oriented posterobuccally. The associated striid on the lingual side of the tooth is very short (approximately one-eighth the remaining crown height) and would soon disappear after only a little more wear. The posterior half of the tooth is dominated by a transversely elongated hypofoesettid. There are two bends in the hypofoesettid, giving it a zig-zag shape. Posterior and lingual to the hypofoesettid is a minute foesettid that is oriented obliquely.

The anterior lower molars are three-rooted, with one posterior and two smaller anterior roots. They are nearly square in occlusal outline. Only one flexid, the hypoflexid, remains open to near the base of the crown. On all other specimens the only lingual flexid is the mesoflexid on one specimen (UNSM 101775). There is no evidence of the parafoesettid or metafoesettid communication with the lingual margin of the tooth on any of the available specimens. The parafoesettid is transversely elongated and the only foesettid on the anterior half of the tooth. It has several subtle bends in it, giving it an irregular shape. In one specimen, UNSM 101661, the buccal end of the parafoesettid is separated from the rest of the foesettid, and forms a small, obliquely oriented foesettid. The mesofoesettid is straight and extends a little over half of the width of the tooth. It is oriented slightly anterobuccally. The hypoflexid extends about half the width of the tooth and is posterolingually oriented, paralleling the mesofoesettid. A short metafoesettid is the only feature of the posterior half of the tooth. It is mostly parallel with the mesofoesettid, but has a bend near its buccal end, similar to the metafoesettid in P₄.

The last lower molar is essentially identical to the anterior molars except it is narrower and longer.

P⁴ is the largest of the upper cheek teeth. The only persistent flexus is the hypoflexus, the hypostria extending nearly to the base of the crown. On UNSM 101666 the mesoflexus has remained open, but the mesostris extends less than one-fourth of the remainder of the crown height, indicating that the flexus would close after only a little more wear. There is no indication of a parastris or metastris on either of the available specimens. The hypoflexus is oriented in an anterobuccal direction and extends about one-third the width of the tooth. Its buccal end abuts the lingual end of the parafoesette. The parafoesette follows the direction of the hypofoesette, is transversely elongated, and retains some minor irregularities along its enamel outline. On UNSM 101666 there is a minute enamel foesette anterior to the parafoesette. It appears that this accessory foesette would erode after only a little more wear. The mesofoesette (or mesoflexus) extends nearly the entire width of the tooth and curves posteriorly, ending along the posterior margin of the tooth. The metafoesette is short and obliquely oriented.

The upper molars are similar to P⁴ in occlusal pattern but smaller in size, being greatly shortened anteroposteriorly. There is no evidence of buccal striae on any of the referred upper molars. The mesofoesette is long, posteriorly curved, and meets the posterior wall of the tooth. The parafoesette and metafoesette are small and placed as in P⁴. The hypoflexus, again, is oriented as in P⁴.

Discussion.—The type specimen of *Hystricops venustus* is an isolated lower premolar and lower molar, USNM 1180, from the “Niobrara River fauna” of northcentral Nebraska (Leidy, 1858; Stirton, 1935). The single P₄ from Pratt Quar-

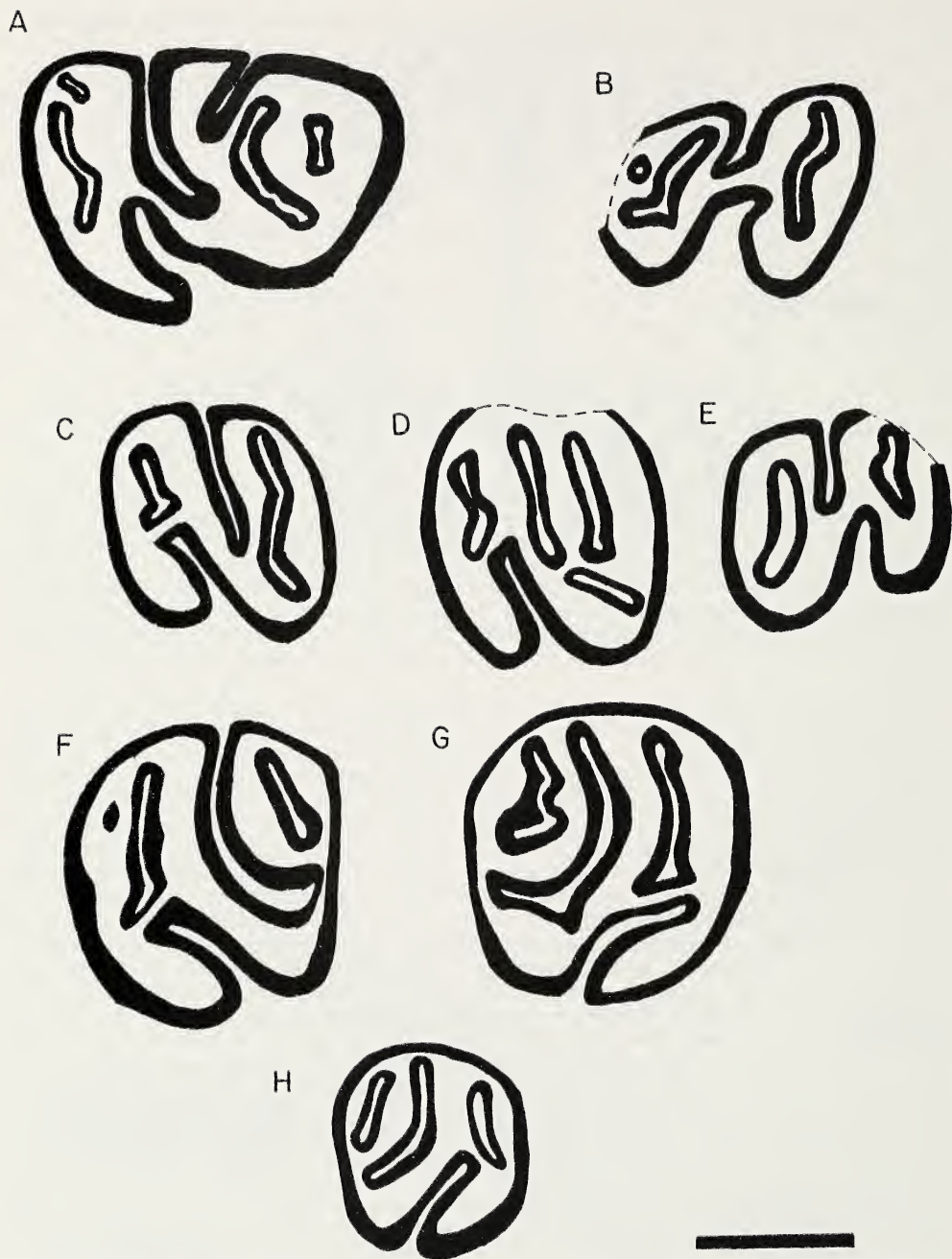


Fig. 6.—Cheek teeth of *Hystricops venustus*. A, UNSM 101660, right P₄. B, holotype, USNM 1180, left P₄. C, UNSM 101775, right M₁ or M₂. D, UNSM 101661, right M₁ or M₂. E, UNSM 101667, left M₃. F, UNSM 101666, left P₄. G, UNSM 101665, right P₄. H, UNSM 101668, right M¹ or M². Bar scale = 5 mm.

Table 6.—Dental measurements of *Hystricops venustus* from Pratt Quarry. Abbreviations as in Table 1. Measurements in mm.

UNSM No.	Isolated Cheek Teeth													
	P ₄			M ₁ or M ₂			M ₃			P ⁴			M ¹	
	a-p	tra	trp	a-p	tra	trp	a-p	tra	trp	a-p	tra	trp	a-p	tr
101660	11.90	7.65	9.11											
101661				7.59	8.14	8.33								
101662				8.00	8.00	7.33								
101775				7.45	8.01	7.14								
101663							7.35	6.51	6.16					
101664							—	5.80	5.84					
101667							5.86	5.80	5.68					
101665										8.50	9.39	8.82		
101666										8.42	9.42	8.65		
101668													6.32	6.51
101669													5.74	7.00

ry (UNSM 101660) is similar in size to the holotype premolar and differs only in the presence of a small reentrant valley on the lingual side of the tooth anterior to the mesoflexid and the minute accessory fossettid lingual to the metafossettid. It appears that this accessory valley and the accessory fossettid would be worn away after only slightly more wear. This is evident on the short flexid because there is no striid on the lingual side of the tooth continuous with it. The remainder of the occlusal morphology is nearly identical with the holotype.

The lower molars referred here to *H. venustus* have all of the lingual flexids closed early in wear, and are nearly identical to the isolated molar included in the holotype of *H. venustus* (Stirton, 1935:fig. 60). The reference of the Pratt Quarry material to *H. venustus* is almost certain. There are no known castorids of this size and morphology reported from the lower horizons (medial to late Barstovian) in the Niobrara River valley of northcentral Nebraska, even though they have been extensively collected and described (Voorhies, 1990b).

The morphology of the upper premolars is also nearly identical to the unnamed species of *Hystricops* reported from the Clarendonian of Oregon (Shotwell and Russell, 1963). The Hemphillian *H. browni* from Oregon (Shotwell, 1963) is also similar in occlusal morphology to the upper premolars referred to *H. venustus* from Pratt Quarry, but differs in the depth of the striae. This similarity verifies the assignment of these later Tertiary beavers to *Hystricops*.

There is also a great similarity in the morphology of the cheek teeth of *H. venustus* to those of an unnamed castorid from the Hemingfordian of Colorado referred by Wilson (1960) to ?*Anchitheriomys* sp. (KU 10173). It appears that the Colorado specimen is also referable to *Hystricops* rather than *Anchitheriomys*. Some of the skull characters of the Colorado skull also differ from those of *Anchitheriomys* (Korth and Emry, 1997). Dorsally, the nasals extend farther posteriorly than the premaxillary bones, a character only otherwise present in *Agnotocastor* and *Neotocastor* among castorids (Korth, 1996a). Likewise, the rostrum is more elongated than in typical castorids, another feature of *Agnotocastor* and *Neotocastor*.

Besides being referable to *Hystricops*, the Hemingfordian skull from Colorado appears to relate this genus to the *Agnotocastorinae* (Korth, 1996a; Korth and

Emry, 1997). However, a detailed description and study of the Colorado specimen is necessary before such an allocation can be made.

Family Eomyidae Deperet and Douxami, 1902

Pseudotheridomys Schlosser, 1926

cf. *Pseudotheridomys* sp.

(Fig. 8A)

Referred Specimen.—UNSM 101748, right mandible with fragment of lower incisor and alveoli for all cheek teeth.

Description.—The mandible is small (alveolar length of cheek teeth = 3.5 mm) and nearly complete, lacking only the base and the posterior processes (coronoid, condyle, and angle). There are alveoli for four cheek teeth: the premolar was two-rooted and the molars three-rooted (one posterior, two anterior). The masseteric scar ends anteriorly below the anterior root of the premolar in a V-shape. On the ascending ramus, the base of the incisor is a lateral bulge that tapers posteriorly to a small ridge. The diastema is shorter than the tooth row and concave. The mental foramen is near the dorsoventral center of the mandible, below the center of the diastema.

Discussion.—Only three genera of eomyids persist in North America into the Barstovian and later times—*Leptodontomys*, *Kansasimys*, and *Pseudotheridomys* (Korth, 1994:161). Of these only *Leptodontomys* and *Pseudotheridomys* are similar in size to UNSM 101748 from Pratt Quarry. UNSM 101748 most closely resembles the mandible of *Pseudotheridomys* because of the more anterior extent of the masseteric scar, shorter diastema, morphology of the base of the incisor on the ascending ramus (low, shelf-like structure on *Leptodontomys*), and the alignment of the alveolar margin of the cheek teeth with the alveolus of the incisor. Engesser (1979:fig. 7a) described the mandible of *Leptodontomys* in detail and noted that the alveolar margin of the cheek teeth generated a line that, if extended anteriorly, would pass the incisor well above its alveolus. In UNSM 101748 and other species of *Pseudotheridomys* this line would be level with the incisor alveolus.

In size, UNSM 101748 is nearly identical to *P. pagei* from the Barstovian of Oregon (Shotwell, 1967a). However, the lack of cheek teeth does not allow a for a definite specific identification of the Pratt Quarry specimen.

Previously, the last reported occurrence of *Pseudotheridomys* in North America was the Barstovian (Engesser, 1979; Fahlbusch, 1979). The recognition of this genus in the late Clarendonian greatly extends its record in North America. In Europe, *Pseudotheridomys* disappears even earlier in the fossil record (Fahlbusch, 1979). Because UNSM 191748 was recovered from the base of the channel at Pratt Quarry, it is possible that it is reworked from the Barstovian layers of the Valentine Formation below the channel. However, there is no previous record of *Pseudotheridomys* from the Valentine Formation (Klingener, 1968; Korth, 1979; Voorhies, 1990b).

Family Heteromyidae Gray, 1868

Subfamily Mioheteromyinae Korth, 1997

Mioheteromys Korth, 1997

Mioheteromys sp., cf. *M. agrarius* (Wood, 1935)

(Fig. 7A, 8B)

Referred Specimens.—UNSM 101750, isolated P⁴; UNSM 101573, partial mandible with lower incisor.

Measurements.—UNSM 101750, a-p, 1.67 mm; tra 0.96 mm; trp, 1.56 mm.

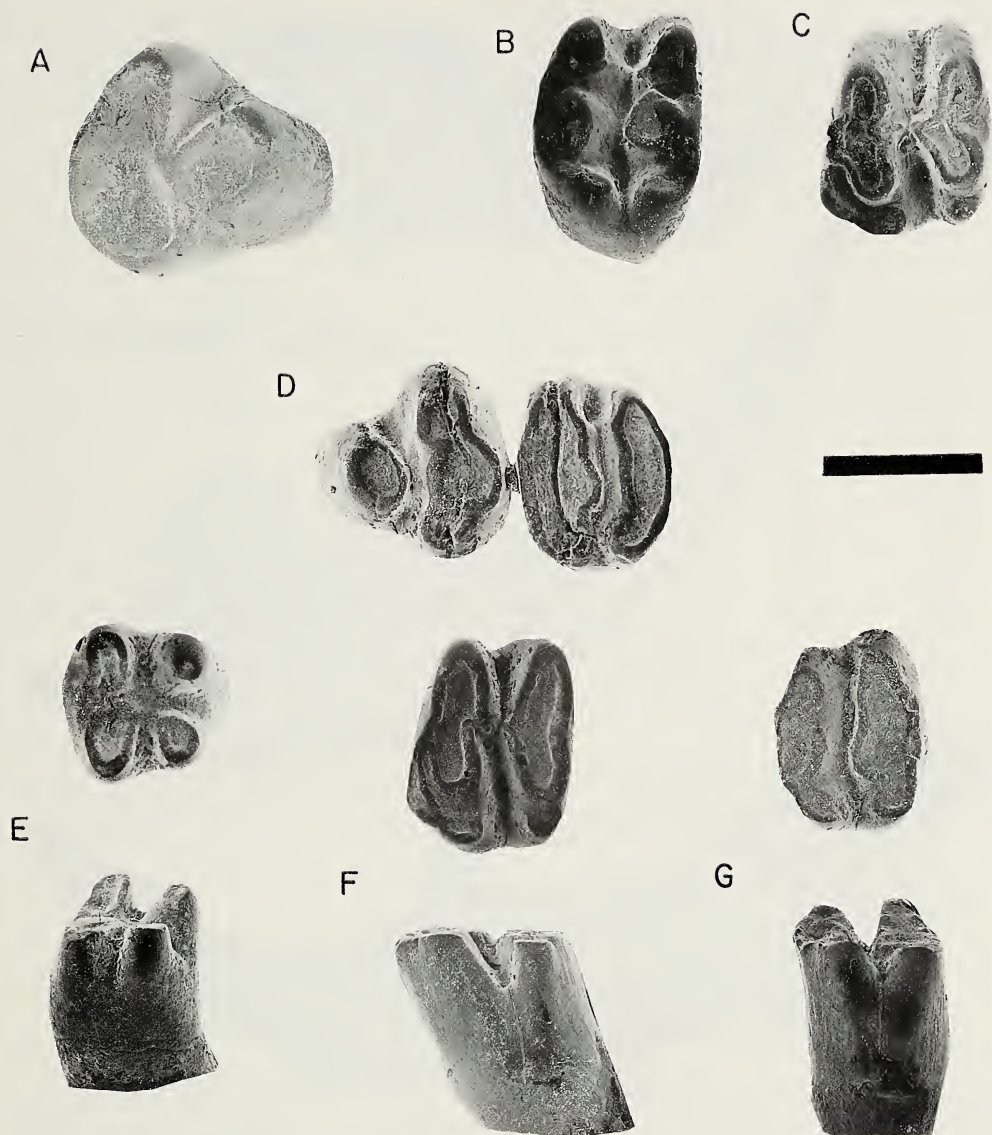


Fig. 7.—Scanning electron micrographs of cheek teeth of heteromyid rodents from Pratt Quarry. A, *Mioheteromys* sp., cf. *M. agrarius*, right P^4 , UNSM 101750. B, C, *Lignimus* sp. B, right M^1 or M^2 , UNSM 101576. C, left M^1 or M^2 , UNSM 101531. D–G, *Cupidininus prattensis*. D, left P^4 – M^1 , UNSM 101502. E, Holotype, left P^4 (occlusal view above, lingual view below), UNSM 101501. F, left M^1 or M^2 (occlusal view above, buccal view below), UNSM 101512. G, right M^1 or M^2 (occlusal view above, lingual view below), UNSM 101510. Bar scale = 1 mm.

Discussion.—A single isolated heteromyid P^4 is distinct from the *Cupidininus* specimens from Pratt Quarry because of its larger size and lower crown height. The union of the protocone to the metaloph is also lingual rather than central as in *Cupidininus*. All of these distinctive characters are typical of *Mioheteromys*. The size of the specimen is comparable with P^4 s of *M. agrarius* from the early and middle Clarendonian of Nebraska (Korth, 1997).

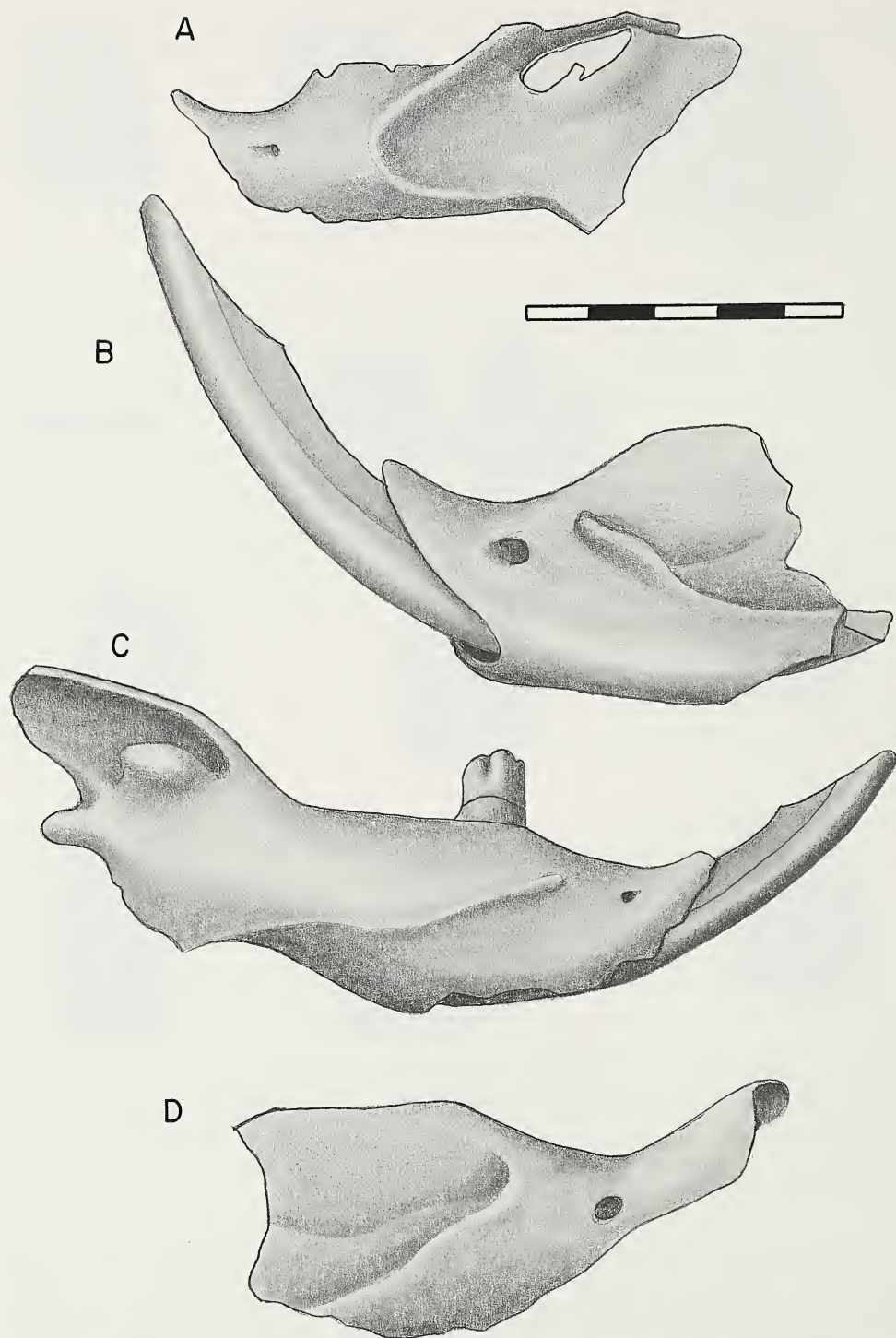


Fig. 8.—Mandibles of geomyoids from Pratt Quarry. All lateral views. A, cf. *Pseudotheridomys* sp., UNSM 101748. B, *Mioheteromys* sp., cf. *M. agrarius*. C, *Cupidinimus prattensis*, holotype, UNSM 101501. D, *Lignimus* sp., UNSM 101532. Bar scale = 5 mm.

Table 7.—Dental measurements of *Cupidinimus prattensis*. Abbreviations as in Table 1. Additional abbreviations (crown height variables from Barnosky, 1986a): CHEV, height of enamel chevron on lingual side of upper molars; LEH, buccal enamel height of lower molars; LEHP, buccal enamel height of lower premolar; T, maximum transverse width; TOTH, crown height of lingual side of upper molars; TP, transverse width of P₄.

		<i>n</i>	M	OR	<i>s</i>	CV
P ₄	a-p	1	0.91			
	tra	1	0.84			
	trp	1	0.91			
	LEHP	1	0.48			
	LEHP/TP	1	0.53			
M ₁ or M ₂	a-p	4	1.15	0.98–1.26	0.12	10.4
	tra	4	1.44	1.33–1.59	0.11	7.7
	trp	4	1.34	1.24–1.49	0.11	8.1
	LEH	3	0.65	0.54–0.73	0.10	16.1
	LEH/T	3	0.44	0.38–0.47	0.05	11.3
P ⁴	a-p	11	1.41	1.28–1.55	0.10	7.0
	tra	11	0.75	0.67–0.83	0.04	6.0
	trp	11	1.33	1.20–1.43	0.08	6.2
M ¹ or M ²	a-p	7	1.06	0.95–1.24	0.10	9.8
	tra	7	1.32	1.16–1.43	0.10	7.7
	trp	7	1.26	1.15–1.34	0.07	5.5
	CHEV	7	0.19	0.13–0.28	0.06	30.4
	TOTH	6	0.88	0.73–0.97	0.09	10.7
	CHEV/T	7	0.14	0.09–0.23	0.05	33.9
	TOTH/T	6	0.64	0.53–0.70	0.06	9.7

The partial mandible preserves the alveoli for P₄ and M₁ only. The rest of the mandible posterior to M₁ is missing. It does not differ from the mandible of *M. agrarius* described previously (Wood, 1935; Korth, 1997).

Subfamily Dipodomyinae Gervais, 1853

Cupidinimus Wood, 1935

Cupidinimus prattensis, new species

(Fig. 7D–G, 8C; Table 7)

Type Specimen.—UNSM 101501, right mandible with I₁ and P₄.

Referred Specimens.—UNSM 101502, maxilla with P⁴–M¹; UNSM 101528, edentulous maxilla; UNSM 101503–101509, 101513, 101519, 101521, isolated P⁴; UNSM 101510, 101511, 101514, 101515, 101520, isolated M¹ or M²; UNSM 101512, 101517, 101529, 101530, isolated M₁ or M₂; UNSM 101522–101527, mandibles lacking cheek teeth.

Diagnosis.—Intermediate sized, smaller than *C. kleinfelderi*, *C. avawatzensis*, *C. quartus*, and *C. bidahochiensis*, larger than *C. eurekaensis* and *C. lindsayi*; lower crowned than *C. nebraskensis*, *C. whitlocki*, and *C. halli*, higher crowned than *C. kleinfelderi*, *C. boronensis* and *C. smaragdinus* with better-developed enamel chevrons on upper molars; also differs from *C. whitlocki* in having a relatively longer P⁴; differs from *C. saskatchewanensis* in lacking the central anteroposterior loph on P₄; differs from *C. tertius* and *C. cuyamensis* in lacking accessory cusps on protoloph of P⁴; differs from *C. nebraskensis* and *C. madisonensis* in having M¹ as wide as P⁴ rather than having P⁴ wider than M¹.

Etymology.—Latin, *-ensis*, suffix meaning from; allusion to Pratt Quarry.

Description.—The only known P₄ of *C. prattensis* is in the holotype. It is simple in occlusal mor-

phology, consisting of only four cusps with no accessory cusps. The crown-height index of the specimen (LEHP/TP) is 0.53, intermediate among species of *Cupidinimus* (Barnosky, 1986a:fig. 12). The cusps of the metalophid (protostylid, metaconid) are nearly equal in size and essentially round in outline. The hypolophid cusps (hypoconid, entoconid) are also equal in size but are oval in outline, the long axis being transversely oriented. The two lophi fuse at the center of the tooth.

The upper premolar on the only maxillary specimen (UNSM 101502) has a transverse width equal to that of M¹. P⁴ is longer (anteroposteriorly) than wide in nearly all specimens. The protoloph is made of a single round to oval protocone. None of the specimens of P⁴ have any accessory cusps on the protocone. The metaloph of P⁴ is made of three aligned cusps as is typical for the genus. The fusion of the lophi is central.

The occlusal morphology of the molars, again, is typical of the genus, consisting of two rows of three cusps. On the lower molars, the anterior cingulum originates at the protoconid and continues buccally to the protostylid. The anterior cingulum on the upper molars originates at the paracone, passes anterior to the protocone, and ends lingually at the protostyle. The crown height index for the lower molars (LEH/T) averages 0.44, higher than in *C. madisonensis* and *C. lindsayi*, but lower than all the other species measured by Barnosky (1986a:fig. 10). The upper molars have a crown height index (TOTH/T) that averages 0.64, lower crowned than all the species measured by Barnosky (1986a:fig. 13). The index of the height of the enamel chevron (CHEV/T) on the upper molars of *C. prattensis* is also lower than other species previously measured (Barnosky, 1986a:fig. 11).

Discussion.—*Cupidinimus prattensis* has relatively low-crowned cheek teeth, exceeding the crown height of only a few species either not measured or unknown to the last reviewer of the genus Barnosky (1986a): *C. boronensis*, *C. kleinfelderi*, and *C. smaragdinus* (Whistler, 1984; Korth, 1996b). The lack of accessory cusps on either the upper or lower premolars of *C. prattensis* is elsewhere consistent only with specimens of *C. lindsayi*, which is smaller and higher crowned than *C. prattensis* (Barnosky, 1986a).

Among its contemporary species of *Cupidinimus* (*C. quartus*, *C. tertius*, *C. cuyamensis*, and *C. avawatzensis*), *C. prattensis* has lower-crowned cheek teeth. It also lacks the accessory cusps on P⁴ or P₄ of these species. *Cupidinimus prattensis* is also smaller than *C. quartus* and *C. avawatzensis*. The unnamed species of *Cupidinimus* from the Clarendonian Mission fauna of South Dakota is smaller than *C. prattensis* and the figured P₄ appears to have an anterostylid (Green, 1971:text-fig. 2D).

As noted by Barnosky (1986a), the species of *Cupidinimus* from the Great Plains typically have lower-crowned cheek teeth than those from the Rocky Mountains and farther west. *Cupidinimus prattensis* is clearly part of this more eastern radiation of *Cupidinimus*. The remainder of the species in this eastern radiation (*C. nebraskensis*, *C. kleinfelderi*, and *C. smaragdinus*) are also characterized by commonly having accessory cusps on the premolars, especially P₄ (Storer, 1975; Korth, 1979, 1996b; Barnosky, 1986a). *Cupidinimus prattensis* differs from these species in this regard, lacking accessory cusps on either upper or lower premolars. *Cupidinimus prattensis* is similar in size and occurrence of accessory cusps on the premolars to the Barstovian *C. whitlocki* but differs from the latter in having slightly lower-crowned cheek teeth and having P⁴ longer than it is wide. *Cupidinimus whitlocki* is diagnosed as having a shortened upper premolar (Barnosky, 1986a).

The recognition of *Cupidinimus prattensis* increases the number of Clarendonian species of this genus to five (see Korth, 1994:186). This is a decrease from the nine Barstovian species, and part of the trend toward the diminishing numbers of species of this genus into the Hemphillian, where only a single species is recognized (Baskin, 1979).

?Subfamily Harrymyinae Wahlert, 1991

Lignimus Storer, 1970

Lignimus sp.

(Fig. 7B, C, 8D)

Referred Specimens.—UNSM 101531, isolated M_1 or M_2 ; UNSM 101516, 101533, isolated M^1 or M^2 ; and UNSM 101532, partial edentulous mandible.

Measurements.—Lower molar (UNSM 101531): a-p, 1.22 mm; tra, 1.32 mm; trp, 1.35 mm. Upper molars: UNSM 101516, a-p, 1.19 mm; tra, 1.43 mm; trp, 1.39 mm; UNSM 101533, a-p, 1.26 mm; tra, 1.75 mm; trp, 1.71 mm.

Description.—The cheek teeth are nearly identical in morphology to those of *Lignimus montis* and *L. austridakotensis* except in size. The mandible referred to *Lignimus* is robust for a heteromyid. The diastema is shallow and long. The masseteric scar has a strong ventral ridge that extends to a point just anterior to the roots of P_4 , near the center of the mandible. At its anterior end it curves posteriorly. There is a very faint ridge marking the dorsal margin of the masseteric fossa that disappears below the alveolus for M_1 . The mental foramen is small and directly anterior to the end of the masseteric ridge.

Discussion.—The specimens referred here to *Lignimus* are intermediate in size between *L. montis* and *L. austridakotensis* from the Great Plains (Storer, 1975; Korth, 1996b). The cheek teeth are not transversely elongated as in *L. transversus* from Wyoming (Barnosky, 1986b).

The mandible of *Lignimus* has never before been described. The allocation of the Pratt Quarry specimen to *Lignimus*, even though it lacks cheek teeth, is based on its comparable size with the cheek teeth identified as *Lignimus* and a lack of any other geomyoid in the fauna to which it could be allocated. The most intriguing character of the mandible is the masseteric scar. It is not typical of heteromyids with a small shelf that extends anterior to the tooth row, but is nearly identical to the masseteric scar on the mandible of the harrymyine *Harrymys irvini* (Wahlert, 1991:fig. 1). This similarity of the mandible reinforces the suggestion that *Lignimus* belongs in the Harrymyinae rather than any other group of geomyoid.

Lignimus is one of several species present at Pratt Quarry that is known elsewhere only from much earlier horizons (early to middle Barstovian) and thus these specimens might simply be reworked from the lower horizons present at Pratt Quarry. Once again, this is not likely because *Lignimus* specimens are known from the fossiliferous horizon 10 m above the basal channel and are not conspecific with any of the named species of the genus from the Barstovian.

Family ?Geomyidae Bonaparte, 1845

Phelosacomys Korth and Reynolds, 1994

Phelosacomys hibbardi (Storer, 1973)

(Fig. 9, Table 8)

Lignimus hibbardi Storer, 1973.

Parapliosacomys hibbardi (Storer) Korth, 1987.

Phelosacomys hibbardi (Storer) Korth and Reynolds, 1994.

Referred Specimens.—UNSM 101561, 101773, P_4 ; UNSM 101577, isolated dP_4 ; UNSM 101562, 101570, isolated P^4 s; UNSM 101563–101569, 101571, 101574–101576, isolated molars; UNSM 101572, isolated upper incisor.

Description.—The dP_4 referred to *P. hibbardi* is low crowned and the roots are splayed. The tooth is much longer than any P_4 referred to the species. The hypolophid is made of four cusps that fuse together to form a wide loph. The largest cusps recognizable on the hypolophid are the hypoconid and entoconid, the former being the largest. A small hypoconulid is present posterior to the junction of the two main cusps. Buccal to the hypoconid is a small hypostylid. Anterior to the entoconid is a deep valley that separates the entoconid from the large, round metaconid. The remainder of the tooth



Fig. 9.—Scanning electron micrographs of cheek teeth of *Phelosacomys hibbardi* from Pratt Quarry. A, left dP_4 , UNSM 101577. B, left P_4 (occlusal view above, lingual view below), UNSM 101773. C,

is surrounded by a series of seven small cuspsules that run along the buccal and anterior sides of the tooth and on the lingual side anterior to the metaconid. A small triangular cusp is located just anterior to the hypoconid in the center of the tooth.

Of the two P_4 s represented from Pratt Quarry, one is unerupted (UNSM 101561) and the other is relatively well worn (UNSM 10173). On the unerupted tooth all cusps are visible. The metaconid and protostylid are nearly equal in size. There are two small anterostylids present, the lingual one is attached to the metaconid. Together these four cusps form an anteriorly convex lophid, isolating a central basin. The hypolophid is straight and made of two major cusps (entoconid, hypoconid) and a smaller, central hypoconulid. On the worn tooth the cusps have been lost on the occlusal surface and only a small enamel lake is present near the center of the tooth. On the sides of the unworn specimen there is a distinct dentine tract. The ratio of the dentine tract height (measured on the buccal side) to the posterior width of the tooth is 1.41. There are no roots evident on the worn P_4 .

As with the lower premolars, of the two P^4 s referred here to *P. hibbardi*, one is essentially unworn (UNSM 101570) and the other is well worn (UNSM 101562). On the unworn specimen there are three cusps of the metaloph that form a posteriorly convex arc (metacone, hypocone, hypostyle). The protoloph is narrower (buccolingually) than the metaloph and straight. It is made of two cusps, a larger protocone and a smaller, lingual protostyle. The lophs unite lingually. On the worn tooth the cusps are no longer distinguishable. The metaloph is still a wider curved loph and the protoloph a straight, shorter loph. The lophs, as in the unworn specimen, unite lingually. On the worn P^4 , the dentine tracts extend well up the sides of the tooth. The dentine tract height/transverse width ratio of this tooth is 75%. Below the base of the enamel there are the beginnings of roots forming on the worn P^4 .

The molars are hypsodont and the occlusal pattern of cusps is worn away on all specimens available, indicating that the cusps are lost at an early stage of wear. On the sides of the teeth there are dentine tracts. The ratio of the height of these dentine tracts to the transverse width of the teeth is 67–89% (mean = 79%). None of the available permanent teeth show any signs of having roots at any time, regardless of the amount of wear.

Discussion.—The small geomyid specimens from Pratt Quarry are clearly referable to *Phelosacomys hibbardi* originally known from the Clarendonian of Kansas as diagnosed by Storer (1973). The only difference in the morphology of P_4 from Pratt Quarry is the presence of two anterostylids rather than three. The dentine tract on the sides of P_4 are also slightly higher in the Nebraska specimens than on those from Kansas. However, these differences are quite minor and are well within any range of variation of a single species.

The upper premolar of *P. hibbardi* has never before been identified. It is quite similar in occlusal morphology to that of *P. shotwelli* from the Clarendonian of California (Korth and Reynolds, 1994). Both *P. hibbardi* and *P. shotwelli* have anteroposteriorly compressed protolophs that form a straight line unlike that of older species where the protocone is more oval in shape (Korth, 1979). *Phelosacomys hibbardi* and the Pratt Quarry specimens differ from *P. shotwelli* in having less well-developed dentine tracts on the cheek teeth, being larger, and having a P_4 that is longer than wide.

The dP_4 of *Phelosacomys* has never been described previously. This tooth differs from those of heteromyids in having a reduced protoconid and numerous cuspsules that line the buccal and anterior sides of the tooth. This type of deciduous lower premolar is more typical of geomyids (Akersten, 1973). Lindsay (1972:fig. 34b) figured the dP_4 of the primitive geomyid *Mojavemys*. This tooth is very similar to dP_4 of *P. hibbardi*. The similarity of the deciduous premolars of these

←

right P_4 (unworn), UNSM 101561. D, left P^4 (occlusal view above, lingual view below), UNSM 101562. E, right P^4 (unworn: occlusal view above, buccal view below), UNSM 101570. Bar scale = 1 mm.

Table 8.—Dental measurements of *Phelosacomys hibbardi* from Pratt Quarry. Abbreviations as in Table 1. Additional abbreviation: *ht/tr*, crown height index (ratio of height of dentine tract to transverse width of tooth). Measurements in mm.

UNSM No.	dP ⁴			P ⁴			M ₁ or M ₂			P ⁴			M ¹ or M ²		
	a-p	tra	trp	a-p	tra	trp	ht/tr	a-p	tr	ht/tr	a-p	tra	trp	ht/tr	trp
101577	2.53	1.25	1.51												
101561				1.81	1.47	1.83	—								
101564								1.28	2.00	0.67					
101565								1.20	1.93	1.00					
101566								1.27	2.08	0.86					
101773				1.87	1.32	1.67	1.41								
101562								1.54	1.04	1.90	0.75				
101563												1.29	2.11	—	
101567												1.19	1.83	0.89	
101568												1.23	1.84	—	
101569												1.15	1.75	0.79	
101570								1.34	1.06	1.84	—				
101571												1.11	1.89	—	

taxa make them more likely geomyids than heteromyids, although their systematic position within the Geomyidae is not certain.

Family Cricetidae Rocheburne, 1883

Subfamily Peromyscinae Hershkovitz, 1966

Tregomys Wilson, 1968

Tregomys shotwelli Wilson, 1968

(Fig. 10A)

Gnomomys saltus Wilson, 1968.

Referred Specimen.—UNSM 101534, isolated right M_1 .

Measurements.—a-p, 1.39 mm; tra, 0.71 mm; trp, 0.90 mm.

Discussion.—The isolated M_1 referred to *Tregomys shotwelli* is nearly identical to M_1 of the holotype from Trego County, Kansas (Wilson, 1968). It is separable from all of the other cricetids from Pratt Quarry in being smaller (except *Copemys pisinnus*), having a central, symmetrical anteroconid (asymmetrical in other species), and lacking the complete alternation of cusps present in *Antecalomys phthanus* (described below). Voorhies (1990b) synonymized *Gnomomys saltus* with *T. shotwelli*. This synonymy is followed here.

Copemys Wood, 1936

Copemys pisinnus Wilson, 1968

(Fig. 10C, D, 11A; Table 9)

Referred Specimens.—UNSM 101535, left mandible with M_1 – M_3 ; UNSM 101536, right mandible with M_1 – M_3 ; and UNSM 101537, right maxilla with M^2 .

Discussion.—The Pratt Quarry specimens referred to *Copemys pisinnus* are inseparable from the topotypic material from Kansas in size and morphology (Wilson, 1968). The molars are simple, lacking mesolophids and other accessory cuspules and lophs. However, these specimens are also very similar to specimens of *C. dentalis* from the Clarendonian of Nevada and Oregon (Hall, 1930; Clark et al., 1964; Shotwell, 1967b). The holotype of *C. dentalis* is slightly larger than specimens of *C. pisinnus* from Kansas and Pratt Quarry (Clark et al., 1964:table 4; Wilson, 1968:table 18; Table 9, this paper), but all of these specimens are within the range of size of a large sample of *C. dentalis* from Oregon (Shotwell, 1967b:table I). The low frequency of accessory lophs and styles on the Oregon material is also compatible with the described material of both *C. pisinnus* and *C. dentalis*.

It is very likely that *C. pisinnus* is a junior synonym of *C. dentalis*. However, no formal synonymy will be proposed here because the type and topotypic material of *C. dentalis* were not available for this study. Direct comparison with the type material of *C. dentalis* is necessary before a definite synonymy can be proposed.

The *Copemys pisinnus* material is distinctly smaller than any of the other *Copemys* species present at Pratt Quarry (described below). Although this material is similar in size to the isolated M_1 referred above to *Tregomys shotwelli*, it differs from the latter in having the *Copemys* morphology of M_1 —asymmetrical anteroconid, and protoconid and metaconid not directly transversely aligned. In *T. shotwelli* the anteroconid is central and symmetrical, and the protoconid and metaconid are directly buccolingually aligned with no hint of alternation.

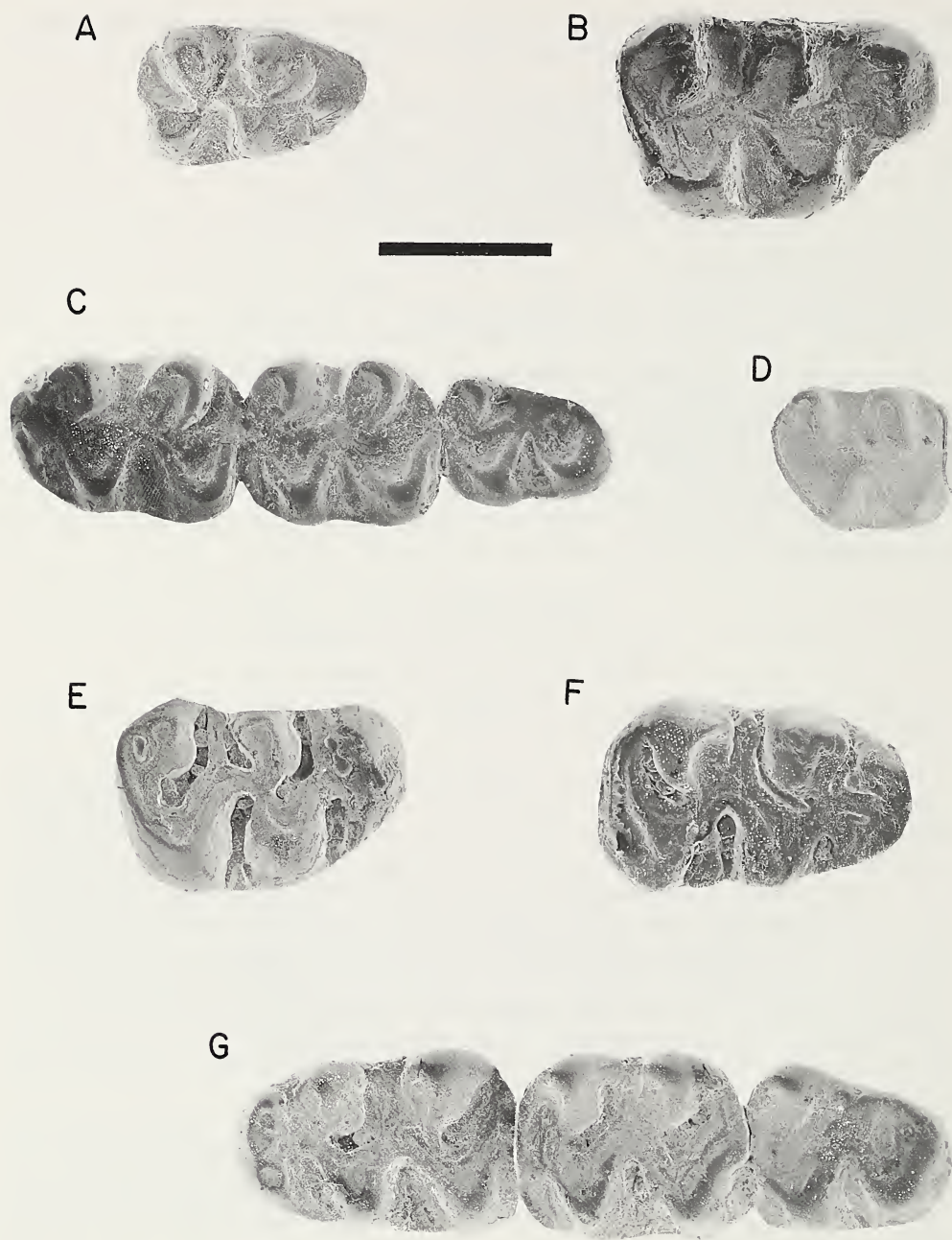


Fig. 10.—Scanning electron micrographs of cheek teeth of *Copemys* and *Tregomys* from Pratt Quarry. A, *Tregomys shotwelli*, right M_1 , UNSM 101534. B, *Copemys* sp., right M^1 , UNSM 101560. C, D, *Copemys pisinnus*. C, left M_1-M_3 , UNSM 101535. D, right M^2 , UNSM 101537. E–G, *Copemys mariae*. E, right M^1 , UNSM 101593. F, right M_1 , UNSM 101541. G, left M_1-M_3 , UNSM 101538. Bar scale = 1 mm.

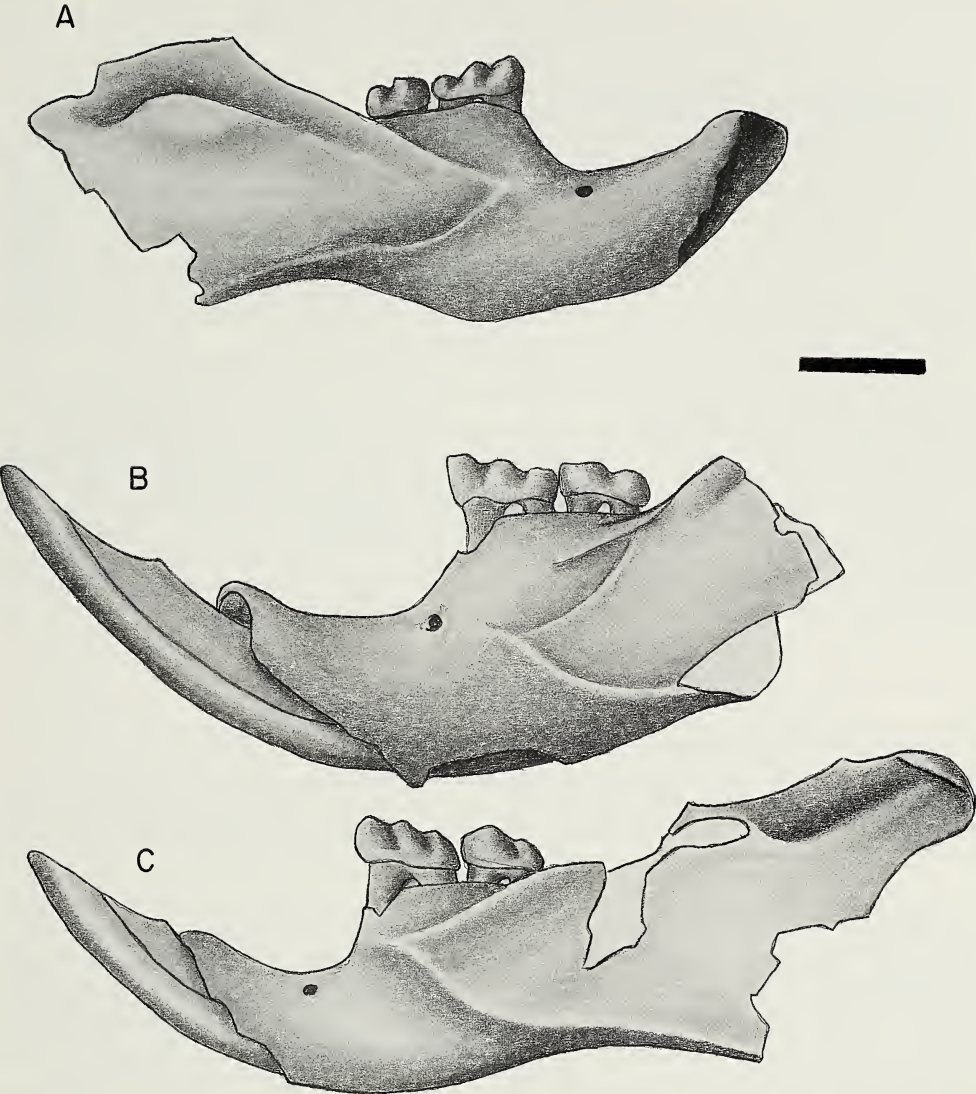


Fig. 11.—Mandibles of cricetid rodents from Pratt Quarry. All lateral views. A, *Copemys pisinnus*, UNSM 101536. B, *Copemys mariae*, UNSM 101539. C, *Antecalomys phthanus*, UNSM 101552. Bar scale = 2 mm.

Table 9.—Dental measurements of *Copemys pisinnus* from Pratt Quarry. Abbreviations as in Table 1. Measurements in mm.

UNSM No.	M ₁			M ₂			M ₃			M ₁ –M ₃	M ²		
	a-p	tra	trp	a-p	tra	trp	a-p	tra	trp		a-p	tra	trp
101535	1.31	0.86	0.99	1.12	0.99	0.96	0.98	0.76	0.70	3.49			
101536	1.48	0.85	1.00	1.19	0.92	0.94							
101537											1.00	0.84	0.84

Copemys sp.

(Fig. 10B)

Referred Specimen.—UNSM 101560, isolated right M¹.*Measurements*.—a-p, 2.00 mm; tra, 125 mm; trp, 127 mm.

Description and Discussion.—UNSM 101560 is considerably larger than any of the other cricetids from Pratt Quarry. The anterocone is weakly doubled, similar to the condition in the Barstovian to Clarendonian *Copemys russelli* (James, 1963; Lindsay, 1972). This tooth differs from *C. russelli* in being larger, lacking a paralophule and mesoloph, and having the protocone attached to the paracone by the protolophule II only. Besides its larger size, UNSM 101560 is distinct from all of the other cricetids from Pratt Quarry. It differs from *C. mariae* by lacking a mesoloph and other accessory lophs; from *Tregomys shottwelli* and *C. pisinnus* by being over 50% larger; and from *Antecalomys phthanus* (described below) in having cusps more directly buccolingually aligned (not alternating) and lacking the accessory root and shallow anterior groove on the anterocone.

In size, UNSM 101560 is closest to the Clarendonian *Copemys esmeraldensis* (Clark et al., 1964: 53). It differs from upper molars of *C. esmeraldensis* in lacking a paralophule and mesoloph and being relatively narrower (buccolingually).

Storer (1975) reported a large sample of *Copemys kelloggae canadensis* (= *C. niobrarenensis*, Voorhies, 1990b) from the Barstovian of Saskatchewan that had a wide range of size and morphology which would include UNSM 101560. However, this sample appears to represent more than a single species because of the high coefficients of variation of the measurements (greater than 10) and extremely different morphologies present. A sample of probable topotypic specimens of *C. niobrarenensis* from Nebraska are clearly smaller than UNSM 101560 (Voorhies, 1990b: table A-10). The Canadian sample is also characterized by a very high percentage of long mesolophs, paralophules, and accessory cusps on M¹, unlike the specimen from Pratt Quarry.

Copemys mariae Baskin and Korth, 1996

(Fig. 10E–G, 11B; Table 10)

Copemys lindsayi Dalquest et al., 1996 (not *C. lindsayi* Sutton and Korth, 1995).

Referred Specimens.—UNSM 101538, left mandible with incisor and M₁–M₃; UNSM 101539, mandible with left M₁–M₂; UNSM 101540, mandible with right M₁–M₂; UNSM 101541, 101791, isolated M₁; UNSM 101792, right M₂; UNSM 101542, fragmentary mandible with left M₂; and UNSM 101593, right M¹.

Amended Diagnosis.—Differs from all species of *Copemys* except *C. esmeraldensis* and *C. barstowensis* in having well-developed mesolophs (-ids) and other accessory lophids on molars, complex anterocones (-ids) on first molars (often doubled) wearing to a broad (buccolingually) anterior loph, and having a mandible with a symphyseal eminence (chin process); differs from *C. esmeraldensis* and *C. barstowensis* in being smaller; a minute accessory root is variably present on M¹.

Description.—The mandible is more robust than other species of *Copemys* except *C. esmeraldensis* (Clark et al., 1964: fig. 9F). Along the ventral margin of the mandible, a small piece of bone has been broken away at the ventral end of the symphysis on all specimens, implying that there was a small eminence there (= "chin process"), similar to the morphology of *C. esmeraldensis*. The masseteric scar extends anteriorly to below the anterior root of M₁. The anterior end of the masseteric scar forms a V-shape. The dorsal ridge of the masseteric fossa is not coincident with the anterior margin of the ascending ramus for its anterior 2 mm. The ascending ramus arises level with M₃. There is a deep valley separating the ascending ramus from the tooth row. The mental foramen is high on the mandible at the posterior end of the diastema. The diastema is fairly deep and steeper on its posterior slope below P₃ than along its anterior slope.

The first lower molar is the largest of the tooth row. The anteroconid is broad and complex, often consisting of two or more cusps. It wears to a broad loph in specimens of older individuals. A loph runs from the anteroconid around the anterobuccal corner of the tooth, ending just anterior to the protoconid. The metalophid cusps unite anteriorly (metalophulid I) and fuse with the anteroconid near the center. The buccal cusps (protoconid, hypoconid) are crescentic, and the lingual cusps (metaconid, entoconid) are anteroposteriorly compressed. The mesolophid is always long, reaching the lingual margin of the tooth. On the buccal side of the tooth there is usually either a small ectostylid

Table 10.—Dental measurements of *Copemys mariae*. Abbreviations as in Table 1. Measurements in mm.

UNSM No.	M ₁			M ₂			M ₃			M ₁ -M ₃	M ²		
	a-p	tra	trp	a-p	tra	trp	a-p	tra	trp		a-p	tra	trp
101538	1.69	0.95	1.12	1.30	1.11	1.08	1.24	0.98	0.75	4.24			
101539	1.74	1.04	1.15	1.44	1.21	1.18							
101540	1.77	1.00	1.14	1.46	1.19	1.16							
101541	1.74	1.19	1.22										
101542				1.33	1.07	0.97							
101791	1.81	0.99	1.12										
101792				1.52	1.22	1.16							
101593											1.79	1.11	1.14

between the protoconid and hypoconid, or a distinct buccal mesolophid. The entoconid fuses with the anterior arm of the hypoconid. The posterior cingulum extends the entire width of the tooth. Dalquest et al. (1996) reported the variable occurrence of a small accessory root on topotypic M₁'s from Oklahoma. There is no indication of these accessory roots on the Pratt Quarry material.

The second lower molar is similar to M₁, lacking only the anteroconid. The metaconid is positioned along the anterior margin of the tooth, from which runs the buccal loph along the anterobuccal corner of the tooth. The mesolophid is long, often ending in a mesostylid. Commonly, there is an ectostylid between the buccal cusps. A distinct hypoconulid is preserved as a widening of the posterior cingulum, just posterior and lingual to the hypoconid.

The last lower molar is the smallest of the lower cheek teeth. Anteriorly, it is similar to M₂. The mesolophid is long and fuses with the posterior cingulum at its lingual end. The hypoconid is reduced and the entoconid is completely lacking. There is no indication of an ectostylid.

M¹ has a complex, broad anterocone. As in M₁, it consists of at least two minute cuspules. There is also a distinct paralophule between the anterocone and paracone. The lingual cusps are crescentic (protocone, hypocone) and the buccal cusps are round but anteroposteriorly compressed. The paracone joins the posterior arm of the protocone. The protocone joins the anterocone near its center by way of an anteroposteriorly directed loph. The mesoloph reaches the buccal margin of the tooth. The metacone joins the posterior cingulum near its center. There is a minute entostyle along the lingual border of the tooth between the lingual cusps. No other upper molars have been recovered.

Discussion.—*Copemys mariae* is based on several isolated cheek teeth from the middle to late Clarendonian of Oklahoma (originally called *C. lindsayi*; Dalquest et al., 1996). The size and morphology of the cheek teeth described here from Pratt Quarry do not differ from the topotypical material, and thus are clearly referable to this species.

Copemys mariae is the largest of the cricetids from Pratt Quarry except for the isolated tooth referred above to *Copemys* sp. Among species of *Copemys*, *C. mariae* most closely resembles *C. barstowensis* and *C. esmeraldensis* from the Barstovian or Clarendonian west of the Rocky Mountains (Clark et al., 1964; Shotwell, 1967*b*; Lindsay, 1972). All three species are characterized by bulbous cusps on the cheek teeth, robust mandibles with a chin process, complex anterocones (-ids) on the first molars, and accessory lophs and cuspules on the molars. These three species, *C. esmeraldensis*, *C. barstowensis*, and *C. mariae*, appear to form a lineage within *Copemys*, distinct from all other species.

Repenning (1968) pointed out several characters of the mandible of arvicolines that separated them from other cricetids, all related to a change in the masseteric musculature that was more advantageous to the propalinal chewing motion of arvicolids. These features were: 1) ascending ramus originates more anteriorly (blocking M₂ laterally) and is steeper; 2) the dorsal margin of the masseteric fossa is posterior to, rather than coincident with, the anterior margin of the ascending

ramus; 3) there is a ventral symphyseal eminence (chin process); 4) there is a deep valley between the tooth row and the ascending ramus; and 5) the ventral margin of the masseteric fossa is shelf-like.

Of these features, three are present in the mandibles of *C. mariae*. The dorsal margin of the masseteric fossa on specimens of *C. mariae* ultimately joins the anterior margin of the ascending ramus, but not along the anterior part below the cheek teeth. This arrangement is nearly identical to that in the early Hemphillian arvicoline *Goniodontomys disjunctus* (Repenning, 1968:fig. 8). The chin process on specimens of *C. esmeraldensis* and *C. mariae* are also part of the arvicoline mandibular construction that is not present in other species of *Copemys*. The third arvicoline feature of the mandible of *C. mariae* is the deep valley between the tooth row and the ascending ramus (temporal fossa).

Dentally, there is nothing about the *C. barstowensis*–*C. esmeraldensis*–*C. mariae* lineage that is particularly reminiscent of the earliest arvicolines. However, the shared characters of the mandible are suggestive of a possible relationship. It has been suggested that at least the earliest subfamily of arvicolids, the Prometheomyinae, was derived from a *Copemys*-like cricetid (Martin, 1975). A North American ancestor for the Prometheomyinae is also suggested by the fact that the earliest arvicolids anywhere are the early Hemphillian prometheomyines *Microtoscopes* and *Goniodontomys* from North America (Repenning et al., 1990). The Clarendonian occurrence of both *C. mariae* and *C. esmeraldensis* from Nebraska and Oregon, respectively, is consistent with the earliest occurrence of arvicolids from the early Hemphillian of the same areas.

The ancestry of the earliest arvicolids (= microtines) is still not certain, but the shared mandibular morphologies of *C. mariae* with these early North American arvicolids supports the hypothesis of a North American origin, at least for the Prometheomyinae.

Subfamily Sigmodontinae Wagner, 1843

Antecalomys, new genus

Peromyscus Gloger, Shotwell, 1967b (in part).

?*Copemys* Jacobs, 1977.

?*Copemys* Korth, 1994.

Type Species.—*Antecalomys phthanus* n. sp.

Referred Species.—*Antecalomys valensis* (Shotwell, 1967b), and *A. vasquezii* (Jacobs, 1977).

Range.—Late Clarendonian of Nebraska, and Hemphillian of Oregon and Arizona.

Diagnosis.—Small sigmodontine, differs from all other sigmodontines in the following characteristics: more weakly divided anterocone of M^1 , anteroconid asymmetrical to weakly divided on M_1 , alternation of cusps incomplete on upper molars (paracone not directly connected to hypocone) but complete on lowers, accessory rootlet on M^1 but not on M_1 , and M^3/M_3 markedly reduced in size relative to second molars; differs from contemporary sigmodontine *Abelmoschomys* in lacking accessory lophs (including mesolophs and mesolophids) and styles on the molars, and having alternation of cusps complete on the lower molars (protoconid and entoconid directly connected).

Etymology.—Latin, *ante*, before; and *Calomys*, possibly related rodent.



Fig. 12.—Scanning electron micrographs of cheek teeth of *Antecalomys phthanus*. A, holotype, left M^1 , UNSM 101543. B, left M^1 – M^3 , UNSM 101545. C, left M_1 – M_2 , UNSM 101552. D, left M_3 , UNSM 101553. Bar scale = 1 mm.

Discussion.—*Antecalomys* differs from contemporary cricetids based on the following dental characters: from *Copemys* Wood (1936) in having a split anterocone and accessory rootlet on M^1 ; from *Abelmoschomys* Baskin (1986) in its smaller size, less ovate first molars, the lack of accessory lophs (-ids) on the molars, and complete alternation of cusps on lower molars; and from *Tregomys* Wilson (1968) by the same characters as for *Copemys* as well as an asymmetrical anteroconid on M_1 (symmetrical in *Tregomys*). *Antecalomys* differs from other Tertiary sigmodontine rodents as follows: anteroconid on M_1 less well divided than in *Symmetrodontomys* and *Calomys* (*Bensonmoms*), anterocone on M^1 less well divided than in *Baiomys* and the former genera, accessory rootlet minute on M^1 but lacking on all M_1 s; cheek teeth much lower crowned than in *Prosigmodon* and *Sigmodon*, and alternation of cusps incomplete on upper molars (complete on other genera).

Antecalomys phthanus, **new species**

(Fig. 11C, 12; Table 11)

Type Specimen.—UNSM 101543, isolated left M^1 .

Referred Specimens.—UNSM 101544, 101546–101551, M^1 s; UNSM 101545, maxilla with M^1 – M^3 ; UNSM 101554, 101555, 101557, isolated M_1 s; UNSM 101556, isolated M_2 ; UNSM 101552, mandible with incisor and M_1 – M_2 ; UNSM 101553, 101558, mandibles with M_3 ; UNSM 101768, mandible with M_1 – M_3 ; and UNSM 101559, edentulous mandible.

Diagnosis.—Largest species of the genus; anterocone on M^1 less well divided than in other species.

Etymology.—Greek, *phthano*, come before or anticipate.

Description.— M^1 is the largest of the upper cheek teeth. The molars decrease in size from M^1 to M^3 . The anterocone on M^1 is transversely broad and buccally placed. A groove along the anterior slope divides the cusp. The depth of the groove is variable but is always present, although it never totally divides the anterocone into two separate cusps. The lingual cusps are crescentic (protocone, hypocone) and the buccal cusps are round to oval in shape (paracone, metacone). The anterior arm of the protocone joins the posterior wall of the anterocone lingual to its center. The paracone fuses with the posterior arm of the protocone just posterior to the posterobuccal corner of the protocone. Posterior to this junction, the central mure bends lingually before it joins the hypocone. The metacone joins the posterior arm of the hypocone just posterior to the posterobuccal corner of the hypocone. The posterior cingulum is extremely short. No specimens of M^1 have any accessory lophs or cuspules. There is never a mesoloph. On the base of the tooth there is always a small to minute accessory root between the two main buccal roots above the paracone.

M^2 is similar to M^1 in the orientation of the cusps but lacks the anterocone. The anterior cingulum runs nearly the entire width of the tooth. The anterior arm of the protocone fuses with the anterior cingulum at its center. The paracone is only very weakly joined to the posterior arm of the protocone. On unworn specimens it appears to be completely isolated. All other features of M^2 are identical to M^1 .

M^3 is the smallest tooth. Only three cusps are recognizable: paracone, protocone, and hypocone. The hypocone is markedly reduced in size. The anterior cingulum is as in M^2 but anterior arms of both the paracone and protocone join the anterior cingulum near its center. The metacone is reduced to a posteriorly convex loph (posterior cingulum) that joins the hypocone lingually.

As with the upper molars, M_1 is the largest of the lower cheek teeth and the molars are progressively smaller from M_1 to M_3 . Again, as in the upper molars, none of the lower molars has a mesolophid or any other accessory lophs or cuspules. The buccal cusps are crescentic (protoconid, hypoconid) and the lingual cusps are oval in shape (metaconid, entoconid). The anteroconid of M_1 is central but asymmetrical. A loph runs from the apex of the cusp down the buccal side and ends posteriorly along the buccal side of the tooth just anterior to the protoconid. The alternation of the cusps is complete. The posterior arm of the protoconid is continuous with the anterior arm of the entoconid. These two cusps are joined by a short, straight, obliquely oriented loph. The anterior arms of both the metaconid and protoconid join the anteroconid near its center. The metaconid is placed anterior to the protoconid. The anterior arm of the hypoconid joins the entoconid directly, just posterior to its junction with the protoconid. The posterior cingulum is short, not reaching the entoconid lingually.

The second lower molar is identical to M_1 except that it lacks the enlarged anteroconid. The metaconid is along the anterior border of the tooth and is continuous with an anterior cingulum that runs anterior to the protoconid, ending buccally before it reaches the protoconid. The arrangement of other cusps is as in M_1 .

The third lower molar is the smallest of the lower cheek teeth. The anterior cusps of M_3 are as in M_2 . The hypoconid is much reduced and the entoconid is totally lacking. The posterior arm of the protoconid extends to the lingual margin of the tooth and encloses a small enamel lake that is formed by the anterior arm of the hypoconid and posterior cingulum.

The mandible is slender. The masseteric scar extends anteriorly to below the anterior root of M_1 in a V-shape. The diastema is relatively short and shallow but has a steep posterior wall below M_1 . The mental foramen is high on the side of the mandible, nearly along the border of the diastema. The ascending ramus arises lateral to M_2 .

The lower incisor is narrow and convex anteriorly. The enamel surface is smooth.

Discussion.—*Antecalomys phthanus* is the most common cricetid from Pratt Quarry. It is intermediate in size between the other cricetids present, larger than *Copemys pisinnus* and *Tregomys shotwelli*, and smaller than *C. mariae* and *Copemys* sp. It also differs from *Copemys* and *Tregomys* as described above. *Antecalomys phthanus* is the oldest and most primitive species of the genus. Both *A. valensis* and *A. vasquezi* are Hemphillian in age and have a deeper groove on the anterior slope of the anterocone of M^1 .

The split anterocone and accessory root on M^1 of *Antecalomys* are diagnostic sigmodontine characters that allow for its allocation to this subfamily. The origin of the New World sigmodontines has been debated as to whether they were immigrant taxa from Eurasia or evolved in North America (see Baskin, 1986, for

review of arguments). The Clarendonian occurrence of *Antecalomys* and its similarity to species of *Copemys* support the arguments for a North American origin for the Sigmodontinae.

Family Zapodidae Coues, 1875

Megasmithus Klingener, 1966

Megasmithus species indeterminate

Referred Specimens.—UNSM 101770, right partial maxilla with M¹; UNSM 101771, right maxilla with alveoli for P⁴–M².

Description and Discussion.—The only tooth preserved is a badly abraded M¹ in UNSM 101770. The size of the tooth (a–p, 1.68 mm; tr, 1.40 mm) is within the range of M¹'s of *M. gladiofex* from the early Barstovian of South Dakota (Green, 1977:1008) and much smaller than those of *M. tihen* from the middle and later Barstovian (Klingener, 1966:table 1; Storer, 1975:87; Green, 1977:1012; Korth, 1980:table 5). Much of the buccal side of the tooth has been removed due to abrasion, thus reducing the transverse measurement. In both species of *Megasmithus*, M¹ is wider than long. It appears that the only reason UNSM 101770 is longer than wide is due to this abrasion.

The occlusal morphology of UNSM 101770 is similar to other species of *Megasmithus* and distinct from species of sicistines in having much more robust, round cusps and a valley that separates the loph connecting the anterocone and protocone and the loph connecting the paracone to the mesocone and hypocone from one another. In contemporaneous sicistines (*Schaubeumys*, *Plesiosmithus*) these lophs are connected by the anterior half of the endoloph which runs from the mesocone to the protocone.

The specimens from Pratt Quarry are far too poorly preserved to be identified specifically. However, this is the latest occurrence of *Megasmithus*, being known only from the Barstovian. Again, as with the specimens of *Pseudotheridomys* and *Lignimus*, it is possible that these two zapodid specimens are reworked from the lower horizons at Pratt Quarry. But once again, these specimens are both from the fossiliferous horizon 10 m above the base of the channel, and thus less likely to have been reworked.

Order Lagomorpha Brandt, 1955

Family Ochotonidae Thomas, 1897

Hesperolagomys Clark, Dawson, and Wood, 1964

Hesperolagomys sp., cf. *H. galbreathi* Clark et al., 1964

Referred Specimen.—UNSM 101709, P².

Measurements.—a–p, 1.37 mm; tr, 2.55 mm.

Description and Discussion.—P² has never been described for any species of *Hesperolagomys*, but UNSM 101709 is similar in size to the topotypic material of *H. galbreathi* from Nevada (Clark et al., 1964). There are two very shallow reentrants on the lingual side of the tooth. The single anterior lobe is roughly circular in outline. Lingual to it is a cement-filled crescentic anterior reentrant. The buccal end of the tooth is broken but the maximum width of the tooth can still be measured. This tooth is similar to P² of *Russellagus* (Storer, 1975:fig. 83F), but is much smaller and the anterior lobe is not flattened anteriorly as in the specimen of *Russellagus*.

The occurrence of *Hesperolagomys* at Pratt Quarry is not unexpected because undescribed specimens of this ochotonid have been reported from other Clarendonian localities in northcentral Nebraska (Voorhies, 1990b).

Russellagus Storer, 1970

Russellagus sp.

(Fig. 13, Table 12)

Referred Specimens.—UNSM 101708, 101776, P³; UNSM 101706, 101707, lower molariform teeth.

Discussion.—The specimens referred here to *Russellagus* differ from those of the Barstovian type species, *R. vonhofi*, only in being slightly larger and lacking plications on the anterior wall of the talonid of lower molariform teeth. The Pratt Quarry material may well represent a distinct species of *Russellagus*, but it is too poorly known to name one at this time.

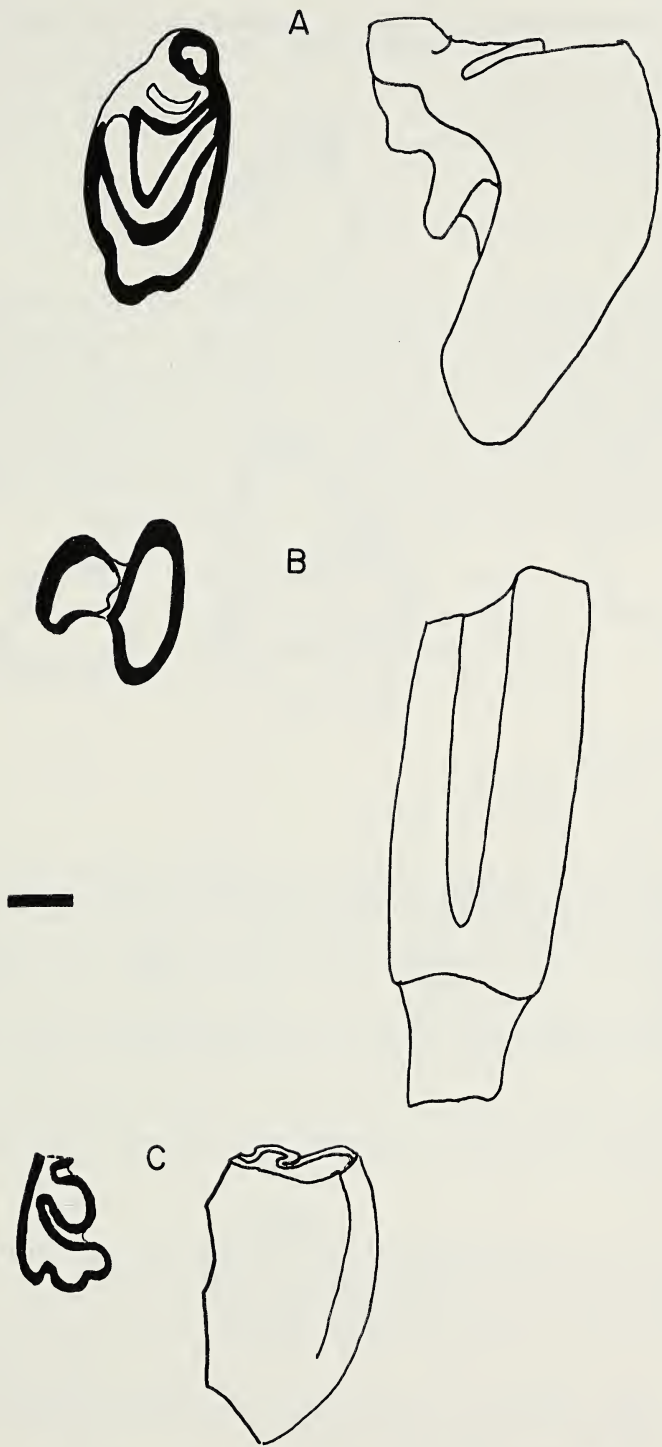


Fig. 13.—Cheek teeth of ochotonids from Pratt Quarry. A, B, *Russellagus* sp. A, left P³ (occlusal view left, anterior view right), UNSM 101708. B, right lower molariform tooth (occlusal view left, buccal view right), UNSM 101706. C, *Hesperolagomys* sp., cf. *H. galbreathi*, right P² (occlusal view left, posterior view right), UNSM 101709. Bar scale = 1 mm.

Table 12.—Dental measurements of *Russellagus* sp. from Pratt Quarry. Abbreviations as in Table 1. Measurements in mm.

UNSM No.	P ₃		Lower molar		
	a-p	tr	a-p	tra	tp
101708	2.05	4.13			
101706			2.35	2.87	1.80
101707			2.31	2.49	1.79

The specimens of *Russellagus*, as with some other species cited from this fauna, are last known from the late Barstovian, and there is no known record in the Clarendonian. This might imply that these specimens were reworked at Pratt Quarry from the Valentine Formation into which the deposit has cut. However, this is not likely the case for *Russellagus* because it has been recovered from all levels of the quarry including the diatomite layer at the top of the section. The lack of *Russellagus* from the Clarendonian in the Great Plains is more likely due to poor sampling for small mammals from rocks of this age.

Family Leporidae Fischer, 1817

Subfamily Archaeolaginae Dice, 1929

Hypolagus Dice, 1917

Hypolagus cf. *H. vetus* (Kellogg, 1910) (Fig. 14A)

Lepus vetus Kellogg, 1910.

Hypolagus vetus (Kellogg), Dice, 1917.

Referred Specimen.—UNSM 101749, right P₃.

Measurement.—a-p, 3.48 mm.

Description and Discussion.—A single isolated P₃ from Pratt Quarry is much larger than any of the other specimens of leporids from this quarry. It is well within the range of size for *H. vetus* (White, 1987:table 2). The lingual edge of the tooth is broken away, so there is no way to determine whether or not there were any internal reentrant valleys. However, the two external reentrant valleys are of similar depth to those of *H. vetus* and lack any complex crenulations as in other species of *Hypolagus* (White, 1987, 1991).

The Barstovian *H. parviplicatus* is similar in size to *H. vetus* (Dawson, 1958; White, 1987; Voorhies, 1990b) but is characterized by shallower anterior and posterior reentrant valleys on P₃. The Pratt Quarry specimen has reentrant valleys equivalent to those of *H. vetus* and deeper than those of *H. parviplicatus*.

UNSM 101749 is the earliest record of *H. vetus* which is otherwise known only from the Hemphillian (Dawson, 1958; White, 1987). Specimens from the Barstovian of Saskatchewan originally referred to *Hypolagus* cf. *H. vetus* (Storer, 1975) were later allocated to *H. parviplicatus* (White, 1991).

Subfamily Leporinae Fischer, 1817

Alilepus Dice, 1931

Alilepus sp.

(Fig. 14B, C; Table 13)

Referred Specimens.—UNSM 101670, partial mandible with right P₃; UNSM 101772, 101784, P₃; UNSM 101671, 101672, 101783, lower molariform teeth; UNSM 101785, P₂; UNSM 101673, 101674, 101786–101788, 101790, 101793, upper molariform teeth.

Description.—The upper and lower molariform teeth referred here resemble those of *Hypolagus* as described elsewhere (Dawson, 1958). One of the P₃s assigned to *Alilepus* is of a very young individual, and the tooth has just come into occlusion (UNSM 101772). The occlusal pattern of the adult speci-

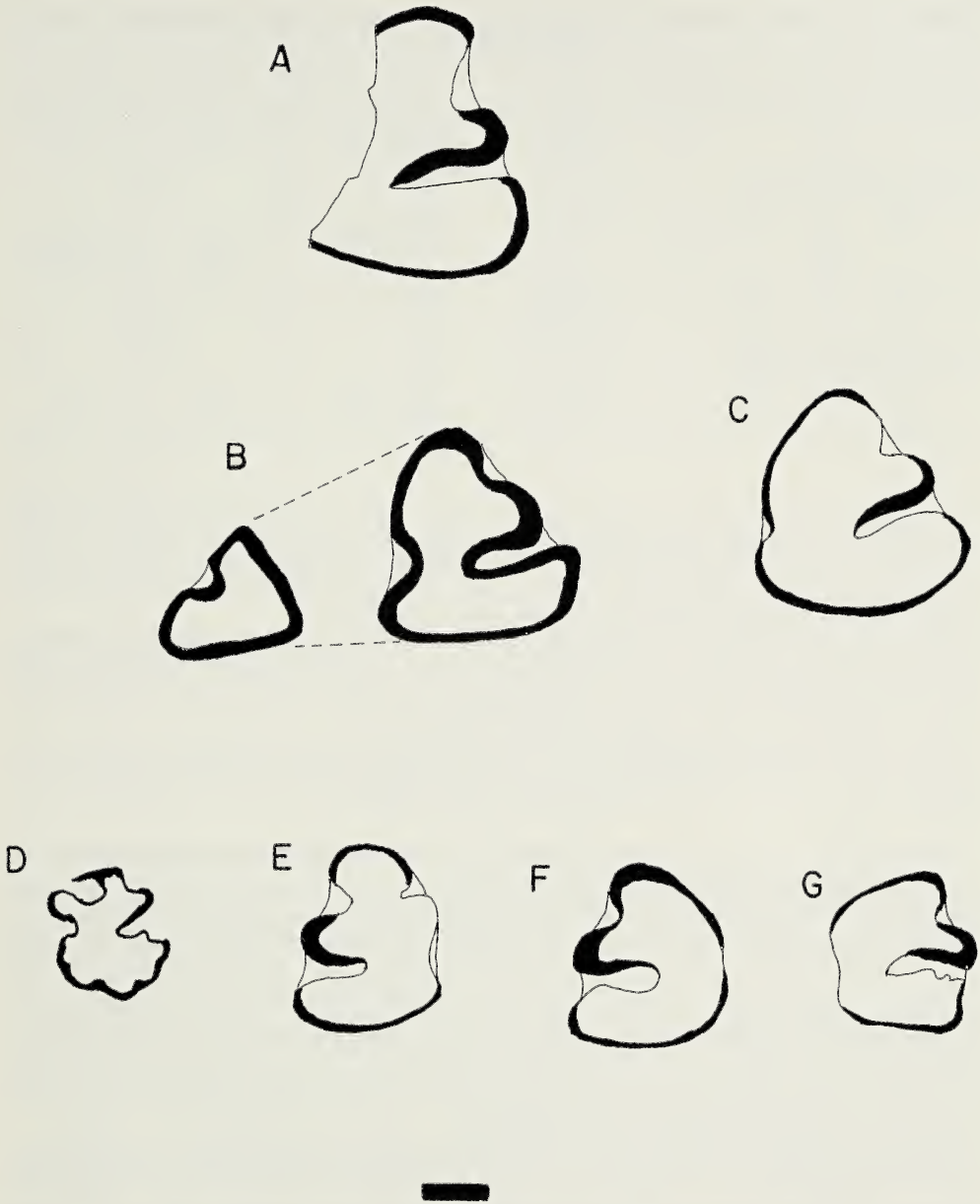


Fig. 14.—Lower third premolars of leporids from Pratt Quarry. A, *Hypolagus* sp., cf. *H. vetus*, right P₃, UNSM 101749. B, C, *Alilepus* sp. B, left P₃, UNSM 101772, occlusal surface (unworn) on left, base of crown on right. C, right P₃, UNSM 101670. D–G, *Pronotolagus whitei*. D, right P₃ (unworn), UNSM 101677. E, Holotype, left P₃, UNSM 101675. F, left P₃, UNSM 101676. G, right P₃, UNSM 101774. Bar scale = 1 mm.

Table 13.—Dental measurements of *Alilepus* sp. from Pratt Quarry. Abbreviations as in Table 1. Measurements in mm.

		n	M	OR	s	CV
P ₃	a-p	3	2.87	2.75–3.00	0.13	4.35
	tr	3	2.80	2.73–2.84	0.06	2.27
Lower molariform teeth						
	a-p	3	2.79	2.73–2.82	0.05	1.86
	tra	3	3.51	3.37–3.58	0.12	3.45
	trp	3	2.85	2.67–3.02	0.18	6.15
P ²	a-p	1	1.69			
	tr	1	3.00			
Upper molariform teeth						
	a-p	7	2.35	2.12–2.62	0.22	9.33
	tr	7	4.07	3.69–4.55	0.30	7.31

mens has two external reentrants. The anterior reentrant is shallow, extending 14% of the total width of the tooth; the posterior reentrant is deeper, extending 45% of the tooth. The posterior external reentrant is oriented just slightly posteriorly. There is a single internal reentrant even with the posterior external reentrant that is cement filled, and continues to the base of the crown. This internal reentrant is quite shallow, extending only 8% of the total width of the tooth.

The nearly unworn P₃ has a simple occlusal pattern with only a single, shallow external reentrant. However, the tooth gradually becomes wider toward its base, and at about half its height, there are two external reentrants and a single internal reentrant. The pattern of the base of the crown of this tooth is nearly identical to that of the adult specimen.

The isolated P² referred to *Alilepus* is similar to that of other species of the genus (White, 1991). There is a main anterior reentrant just lingual to the center of the anterior margin of the tooth that is deep, and curves slightly buccally. Buccal to it is a much smaller reentrant. Both reentrants are cement filled.

Discussion.—The specimens referred here to *Alilepus* fit the diagnosis of the genus (White, 1991:69) by maintaining a distinct posterior internal reentrant along with the two external reentrants on P₃. The Pratt Quarry specimens differ from P₃s of all other species in having the length of the tooth subequal to the width (in all other species this tooth is relatively longer than wide), and having a posterior internal reentrant very shallow. In all other species the posterior internal reentrant of P₃ is nearly as deep as the posterior external reentrant and often closes off lingually to form a small enamel lake. The Pratt Quarry specimens of *Alilepus* are larger than those of *A. wilsoni*, but smaller than the other two North American species of the genus (White, 1991:table 3).

Among species of *Alilepus*, the Pratt Quarry species most closely resembles *A. hibbardi* from the late Clarendonian and possibly early Hemphillian. They differ from *A. hibbardi* in being smaller and having P₃ more square with a shallower posterior internal reentrant. White (1991:fig. 11I) figured an isolated P₃ from the late Clarendonian of California that is similar in the structure of P₃ to the Pratt Quarry specimens. He referred this specimen to *Pronotolagus* sp. The Pratt Quarry specimens are larger than this specimen, and more squared. It is questionable whether the California specimen should be referred to *Pronotolagus* because of its similarity to *Alilepus*. This was also noted by White (1991:81) in his description of the specimen.

The most unusual feature of the P₃s referred here to *Alilepus* is the apparent ontogenetic change from a simple occlusal pattern to a more complex one. The

Table 14.—Dental measurements of *Pronotolagus whitei*. Abbreviations as in Table 1. Measurements in mm.

		<i>n</i>	M	OR	<i>s</i>	CV
dP ₄	a-p	2	1.93	1.92–1.94		
	tra	2	1.90	1.76–2.04		
	trp	2	1.52	1.49–1.55		
P ₃	a-p	5	2.26	2.08–2.42	0.12	5.42
	tr	5	1.92	1.67–2.05	0.15	8.00
Lower molariform teeth						
	a-p	7	2.60	2.26–2.93	0.22	8.50
	tra	7	2.79	2.44–3.02	0.23	8.25
	trp	7	2.40	2.21–2.67	0.18	7.67
M ₃	a-p	3	1.65	1.50–1.87	0.19	11.67
	tra	3	1.68	1.46–1.86	0.20	12.05
	trp	3	1.11	1.05–1.19	0.07	6.50
dP ²	a-p	1	1.20			
	tr	1	1.98			
Upper molariform teeth						
	a-p	8	1.85	1.53–2.11	0.19	10.21
	tr	8	3.34	2.96–3.60	0.25	7.35

species of *Pronotolagus* from Pratt Quarry (described below) shows a very different sequence, from complex to more simplified.

Pronotolagus White, 1991
Pronotolagus whitei, new species
(Fig. 14D–G, Table 14)

Type Specimen.—UNSM 101675, isolated P₃.

Referred Specimens.—UNSM 101678, 101781, dP₄; UNSM 101676, 101677, 101679, P₃; UNSM 101680–101684, 101782, 101789, lower molariform teeth; UNSM 101685, 101778, 101780, M₃; UNSM 101694, dP²; UNSM 101686–101693, 101777, 101779, upper molariform teeth; UNSM 101695, I¹; UNSM 101696, 101705, partial humeri.

Diagnosis.—Near size of *P. apachensis*; differs from *P. apachensis* in having a deeper posterior external reentrant on P₃ (ranging from 50–62% of the width of tooth) and having the posterior reentrant inclined anteriorly rather than posteriorly.

Etymology.—Patronym for John White for his noted work on later Tertiary leporids.

Description.—The occlusal morphology of adult P₃s is similar to those of species of *Hypolagus*. There are two external reentrants. The anterior external reentrant is shallow, extending 17–20% of the width of the tooth and is widely open buccally. The posterior reentrant is deep, ranging from 56–62% of the width of the tooth and angled slightly anteriorly. The lingual margin is either straight or gently concave. The enamel on the lingual side of the tooth is very thin.

The unerupted or juvenile P₃s have two internal and two external reentrants. The external reentrants are similar to those of the adult specimens, but the anterior reentrant is slightly deeper than in the adult specimens (slightly higher than 20% of the width of the tooth) and the posterior external reentrant is slightly shallower than the adult specimens (about 50% of the width). The internal reentrants are shallow, not exceeding 15% of the total width of the tooth. The grooves on the lingual side of the tooth marking the internal reentrants diminish toward the bases of these teeth and are gone at the base of the teeth. The anterior internal reentrant has a narrow lingual opening, whereas the posterior internal reentrant has a broad lingual opening.

The lower molariform teeth (P₄–M₃) resemble those of *Hypolagus* and other leporids. Similarly, the upper molariform teeth (P⁴–M³) resemble those of species of *Hypolagus* as well. No specimens of P³

have been recovered from Pratt Quarry. The hypostriae of the upper molariform teeth, however, differ with wear. On some specimens, the walls of the hypostria are smooth and others are highly crenulated. There are also specimens that show an intermediate morphology, where the walls of the hypostria are smooth for about half of their extent, and then become crenulated.

Discussion.—The range of variation of the internal reentrant valleys on the P_3 s assigned here to *Pronotolagus whitei* is similar to the amount of variation described and figured for the type species of the genus, *P. apachensis* (White, 1991: fig. 11A). The only difference between the Pratt Quarry material and specimens of *P. apachensis* is the depth and orientation of the posterior reentrant valley on P_3 . In *P. apachensis* the posterior external reentrant ranges from 40–49% of the width of the tooth, and is deflected slightly posteriorly. On specimens of *P. whitei*, the posterior external reentrant ranges from 50–62% of the total width of the tooth, and is deflected slightly anteriorly.

It appears that the variation in the depth of the internal reentrant valleys on P_3 of *Pronotolagus* are due to the age of the individual. On specimens with unworn or little-worn teeth, the internal reentrants are the largest, and in older individuals they are lost. On the internal sides of the little-worn P_3 s available from Pratt Quarry, it is evident that the grooves on the internal side of the tooth marking the reentrants become shallower toward the base of the crown. It appears likely that this is also the case with *P. apachensis* which has the same type of variation of the internal reentrants on P_3 (White, 1991:fig. 11A).

The variation in the amount of crenulations in hypostriae of the upper molariform cheek teeth from Pratt Quarry is also consistent with upper cheek teeth referred to *P. apachensis* from its type locality (Wood, 1937). The consistency of the morphology of the upper cheek teeth along with the similarities in the morphology of P_3 make this species clearly referable to *Pronotolagus*.

The recognition of *Pronotolagus* in the late Clarendonian of the northern Great Plains is consistent with its early Hemphillian occurrence elsewhere in Nebraska (White, 1991). The P_3 s from the early Hemphillian LeMoyne Quarry of Nebraska referred to *P. apachensis* (White, 1991:fig. 11B) differ from the Pratt Quarry material in having deeper, more persistent anterior internal reentrants but are similar in having the posterior external reentrant tilted anteriorly rather than posteriorly. The specimens from the Hemphillian may well represent a distinct species of *Pronotolagus* more closely related to *P. whitei* than the type species from California.

CONCLUSIONS

The rodent and lagomorph fauna from Pratt Quarry, represented by 25 species and over 300 specimens, is more diverse than any other from the Clarendonian of the Great Plains (Appendix). Its diversity is even greater than that of any of the Clarendonian microfaunas known from west of the Rocky Mountains (Wilson, 1939; James, 1963; Clark et al., 1964; Shotwell, 1970). Previously, only 12 species of rodents and lagomorphs had been cited from all levels of the Clarendonian of Nebraska (Voorhies, 1990a) and only five had been described (Webb, 1969a). This greater diversity of small mammals gives a much more complete picture of the Clarendonian fauna from the Great Plains.

There are four taxa from the Pratt Quarry that are characteristic of Hemphillian or later faunas: the beaver *Dipoides*, sigmodontine cricetids, the archaeolagine rabbit *Hypolagus vetus*, and leporine rabbits. Of these, leporine rabbits and a single sigmodontine cricetid have been reported elsewhere in North America from

Clarendonian deposits (Baskin, 1986; White, 1991). These first occurrences suggest a latest Clarendonian age for the fauna that consists of otherwise typically Clarendonian rodents and lagomorphs. None of the taxa cited here as first occurrences are immigrants into North America, but rather are more likely to have evolved from earlier North American animals.

The Hemphillian of Nebraska and the Great Plains is well documented so the micromammalian fauna is well known (Hibbard, 1953, 1964; Schultz, 1990; Voorhies, 1990a). These faunas lack a number of taxa present at Pratt Quarry that are characteristic of Clarendonian or earlier ages. This indicates the last occurrence of these taxa: the sciurids *Protospermophilus* and *Petauristodon*, the beaver *Eucastor*, the geomyid *Phelosaccomys*, the heteromyid *Mioheteromys*, the cricetids *Copemys* and *Tregomys*, and the ochotonid *Hesperolagomys*.

Along with the combination of first and last occurrences that indicates a late Clarendonian age for the fauna from Pratt Quarry is a change in the proportions of the rodent fauna that also reflects a time of transition between Clarendonian and Hemphillian ages. The Clarendonian rodent fauna, in terms of diversity of rodent families, is similar to Barstovian faunas in that there is a great diversity of heteromyids and relatively few species of cricetids. In Hemphillian faunas the number of heteromyid species drops drastically and the number of cricetids increases several times (Korth, 1994:table 1). The fauna from Pratt Quarry is clearly transitional in retaining some diversity in the heteromyids, but not as great as in the Barstovian faunas, and having an increase in the diversity of cricetids, although not as great as in Hemphillian faunas.

Four genera described here from Pratt Quarry have been reported previously only from the Barstovian or earlier. All four of these taxa—*Russellagus*, *Lignimus*, *Pseudotheridomys*, and *Megasmithus*—are represented by only a few isolated dental elements in the Pratt Quarry fauna. Of these, *Russellagus* is the best represented, specimens having been recovered from all levels of Pratt Quarry. It might be argued that the specimens representing these taxa are reworked from the lower horizons into which the channel at Pratt Quarry was cut.

While reworking is a possibility, there are several arguments against this suggestion. First, the record of micromammals from earlier Clarendonian horizons in northcentral Nebraska is negligible. There are no other microvertebrate faunas younger than Barstovian and older than Hemphillian in Nebraska (see Voorhies, 1990a), and there are only two other micromammal faunas in the entire Great Plains that are Clarendonian in age (Wilson, 1968; Green, 1971). The occurrence of these small mammals at Pratt Quarry might prove to be continuous if the record of rodents and lagomorphs from early and middle Clarendonian horizons in the Great Plains was better known.

The second argument against reworking is the levels of occurrence at the quarry itself. Both *Russellagus* and *Lignimus* are represented in at least two horizons, not just the basal channel where the obviously reworked bone chips can be found. The specimens of *Megasmithus* are from the fossiliferous level 10 m above the base of the channel, again making it less likely that these specimens were reworked. *Pseudotheridomys* is the only one of these taxa represented from the basal channel at Pratt Quarry only. However, in this case, no specimens of *Pseudotheridomys* have been reported from any quarry in the medial or later Barstovian Valentine Formation in Nebraska (Voorhies, 1990a). The closest geographic occurrence is a possible specimen of *Pseudotheridomys* reported from the medial Barstovian Bijou Hills fauna in South Dakota (Korth, 1996b).

In the case of both *Russellagus* and *Lignimus*, the specimens described above from Pratt Quarry are not assignable to any recognized Barstovian species. If these taxa were identical with the species described elsewhere, it would add support to the reworked hypothesis. However, both of these genera have species that are well represented in the Barstovian of the Great Plains (Storer, 1975; Voorhies, 1990b; Korth, 1996b) but the Pratt Quarry material is distinct from these described species.

Finally, the preservation of the specimens of these previously Barstovian-only taxa from Pratt Quarry does not differ from that of the rest of the fauna. All specimens from Pratt Quarry show some level of abrasion, simply attesting to the fluvial environment in which they were deposited.

Ultimately, it is possible that these four genera of rodents and lagomorphs are reworked from lower horizons at Pratt Quarry. However, it is equally likely, if not more likely, that they are truly a part of the fauna. If, indeed, they are correctly identified as belonging to the Pratt Quarry fauna, then they all represent last occurrences.

Webb (1969b) argued that there were proportionally fewer rodents and lagomorphs from the Clarendonian than from either the Barstovian or the Hemphillian. He believed that the low number of these small herbivores was a true representation of the Clarendonian fauna rather than an artificially reduced number due to factors such as collecting bias. However, with 25 species of rodents and lagomorphs recognized from Pratt Quarry, it appears that the low number of these small mammals previously reported from the Clarendonian was not a true representation of the complete fauna. Preliminary faunal lists presented by Voorhies (1990a) from early and middle Clarendonian localities in Nebraska also suggest that the small herbivore fauna throughout the Clarendonian was much more diverse than suggested by Webb (1969b).

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APPENDIX

Faunal list of rodents and lagomorphs from Pratt Quarry.

Rodentia

Mylagaulidae

Mylagaulus monodon

Sciuridae

Protospermophilus sp., cf. *P. quatalensis*

Ammospermophilus junturensis

Spermophilus (*Otospermophilus*) sp.

cf. *Petauristodon* sp.

cf. *Sciurion* sp.

Castoridae

Eucastor planus

Dipoides tanneri

Hystricops sp., cf. *H. venustus*

Eomyidae

?*Pseudotheridomys* sp.

Heteromyidae

Mioheteromys sp., cf. *M. agrarius*

Cupidininus prattensis

Lignimus sp.

Geomyidae

Phelosacomys hibbardi

Cricetidae

Copemys pisinnus

C. mariae

Copemys sp.

Tregomys shotwelli

Antecalomys phithanus

Zapodidae

Megasminthus sp.

Lagomorpha

Ochotonidae

Hesperolagomys sp., cf. *H. galbreathi*

Russellagus sp.

Leporidae

Pronotolagus whitei

Hypolagus sp., cf. *H. vetus*

Alilepus sp.

THE TRIBE BROSCINI IN MEXICO:
RAWLINSIUS PAPILLATUS, NEW GENUS AND NEW SPECIES
(INSECTA: COLEOPTERA: CARABIDAE),
WITH NOTES ON NATURAL HISTORY AND EVOLUTION

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ABSTRACT

Based on structural and ecological features of adults and larvae, particularly absence of standard fixed dorsal setae in adults, and the habitat of torrential mountain streams, *Rawlinsius papillatus* (type locality: Mexico, Guerrero, Sierra Madre del Sur, 26 km NW El Paraiso, 1800 m) is described as a new monobasic genus and species. This species is placed in the tribe Broscini, subtribe Broscina (Northern Hemisphere assemblage, excluding *Axonya* Andrewes and *Broscodes* Bolivar) on the basis of common possession of the unique set of features used to characterize these higher taxa. A key distinguishes *Rawlinsius* from the other New World genera of Broscini. Separated widely both morphologically and geographically from other New World Northern Hemisphere Broscina, *R. papillatus* is postulated to be a relictual taxon, its present isolation indicating past connections to a more broadly distributed northern broscine lineage.

KEY WORDS: systematics, evolution, biogeography, relicts, Mexico, Coleoptera, Carabidae

INTRODUCTION

Toward evening on 3 July 1982, it got dark. It got dark before lepidopterist John Rawlins had reached his destination higher up in the Sierra Madre del Sur, so he did what he always does in such circumstances. He stopped at the first convenient place, unpropitious as it was, and set up his sheet and traps for a night of serendipitous collecting. It is to this behavior that we owe one of the most extraordinary carabid discoveries of the century.

Always a good general collector, Rawlins wandered from the sheet from time to time to search for other insects. He found an extraordinary tenebrionidlike beetle (Fig. 1, 2, 3A) wading in the water along the shallow edge of a rapid stream just where the stream dropped over a 3-m vertical face. He collected the single female specimen, pinned it, and put it in a box, but its peculiar appearance and behavior remained in his mind.

In the autumn of 1985, Rawlins showed a box of Mexican beetles to Davidson, including the mysterious wading beetle. Much excitement ensued when they realized the beetle belonged in the Carabidae and was of uncertain tribal affinities. Tribes were eliminated one by one until it was decided (based largely on Gestalt) that the beetle belonged in the Broscini or perhaps in a new tribe somewhere in the vicinity of Broscini. But the nearest broscines were several thousand kilometers to the north and south, and, with only a single female, it was impossible to be

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Fig. 1.—Dorsal habitus of *Rawlinsius papillatus*, n. gen., n. sp. Male, total length, ca. 17 mm.

certain. The importance of the discovery seemed to merit an effort to obtain further material, so Rawlins and Davidson returned to the site where the specimen had been found.

They arrived at the site on 8 August 1986 and waited until dark. They approached the wet cliff face (Fig. 3C) and, still a couple of meters away, were excited to see the gun-metal blue glint of several adult beetles (Fig. 3A, B) in the light of the headlamps. Within half an hour, they spotted ten adults and one larva, collecting most of them while leaving a few undisturbed to observe their behavior



Fig. 2.—Ventral habitus of *Rawlinsius papillatus*, n. gen., n. sp. Male, total length, ca. 17 mm.

before collecting them as well. The following night, two more adults and another larva were collected, and no further specimens could be found. Other streams along the road were searched without success. During the ensuing two weeks, several other streams in Guerrero and Oaxaca were searched, also without success.

With 13 adults and two larvae, sufficient material was available for study and dissection. Because of his experience with Broscini and with Mexican Carabidae generally, G. E. Ball was invited to participate in the study of this remarkable species. Examination of the male genitalia (including internal sac) revealed features



Fig. 3.—Photographs of living *Rawlinsius papillatus*, n. gen., n. sp., and of the type locality. A, B, *Rawlinsius papillatus*: A, dorsal aspect; B, dorsal aspect, head and prothorax. C, vertical water-covered rock face, microhabitat of *R. papillatus*, n. gen., n. sp.

indicating an affinity to the tribe Broscini, and other features pointed in that direction. But this seemed unlikely because broscines were not known to occur within several thousand kilometers of southern Mexico. Nonetheless, the authors began with the assumption that the specimens represented an undescribed species that could not be placed in any known genus, but that belonged probably in the Broscini.

To make this species and genus known, we offer the following descriptions and illustrations. We develop a context for understanding these taxa in terms of clas-

sification of the Carabidae (in particular, the Broscini), and in terms of evolutionary, principally biogeographical, considerations.

MATERIALS, METHODS, AND TERMS

Materials

This study is based on examination of 13 adults and two larvae representing a new genus and species. Additionally, material housed in the collections of the Carnegie Museum of Natural History and in the E. H. Strickland Museum, University of Alberta, representing all of the known New World genera of Broscini, was examined.

The two larvae that most probably belong to the new species are discussed briefly in terms of the tribal placement of this species and comparative behavior of larvae and adults. A formal description of the larvae is excluded from this study and will be done separately.

Methods

Techniques

Dissections and illustrations were made using standard techniques, as described, for example, by Shpeley and Ball (1993:10–11).

The only measurements reported are: overall length, the sum of length of head from tip of mandibles to postocular transverse depression + length of pronotum + length of elytra (from basal ridge, along suture) to apex; width is transverse distance across the elytra at their widest point.

Species Recognition and Ranking

In terms of known New World broscines, this taxon was recognized as a new species because of its distinctive combination of structural features. Similarly, the large degree of difference from all other known broscine genera was used to place the species in a genus of its own.

Relationships

These were inferred on the basis of postulated shared derived (synapomorphic) character states (Hennig, 1966:90–91; Ax, 1987:4).

Terms for Structural Features

Most of the words used by us to designate details of structures are recorded in textbooks of general entomology and are used by coleopterists generally. Other words, required to designate particular structural features or parts thereof, are not in general use. We provide information about these words here.

Microsculpture

A “sculpticell” (Fig. 4B:sc) is the space enclosed on the surface of the cuticle by adjacent microlines of the integumental system of microsculpture (Allen and Ball, 1980:485–486).

Body Parts

The term “segment” is restricted to those body parts that reflect embryonic somites; thus, somitelike portions of the abdomen are referred to as segments. Abdominal segments and their appendages are designated by Roman numerals

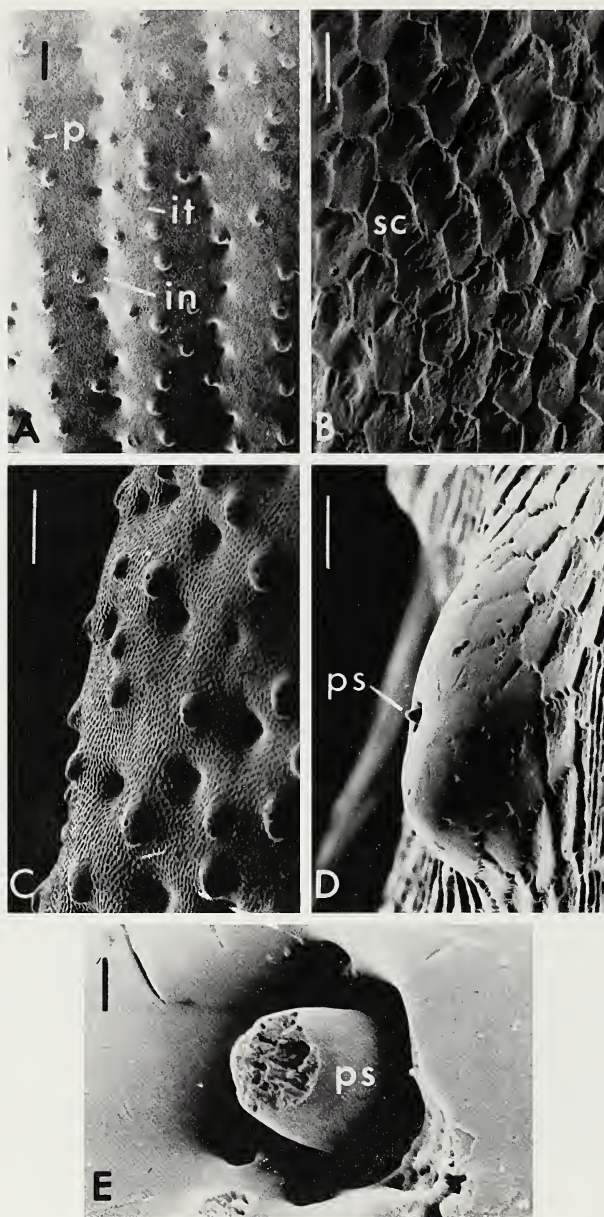


Fig. 4.—SEM photographs of macrosculpture and microsculpture of basal portion of left elytron of *Rawlinsius papillatus*, n. gen., n. sp. A, C, macrosculpture, dorsal aspect, lower and higher magnification, respectively. B, microsculpture, dorsal aspect, mesh pattern. D, papilla, lateral aspect. E, papillar seta, dorsal aspect. Abbreviations: in, stria; it, interval; p, papilla; ps, papillar seta; and sc, sculpticell. Scale bars: A, C = 100 μ m; B, D = 10 μ m; and E = 1 μ m.

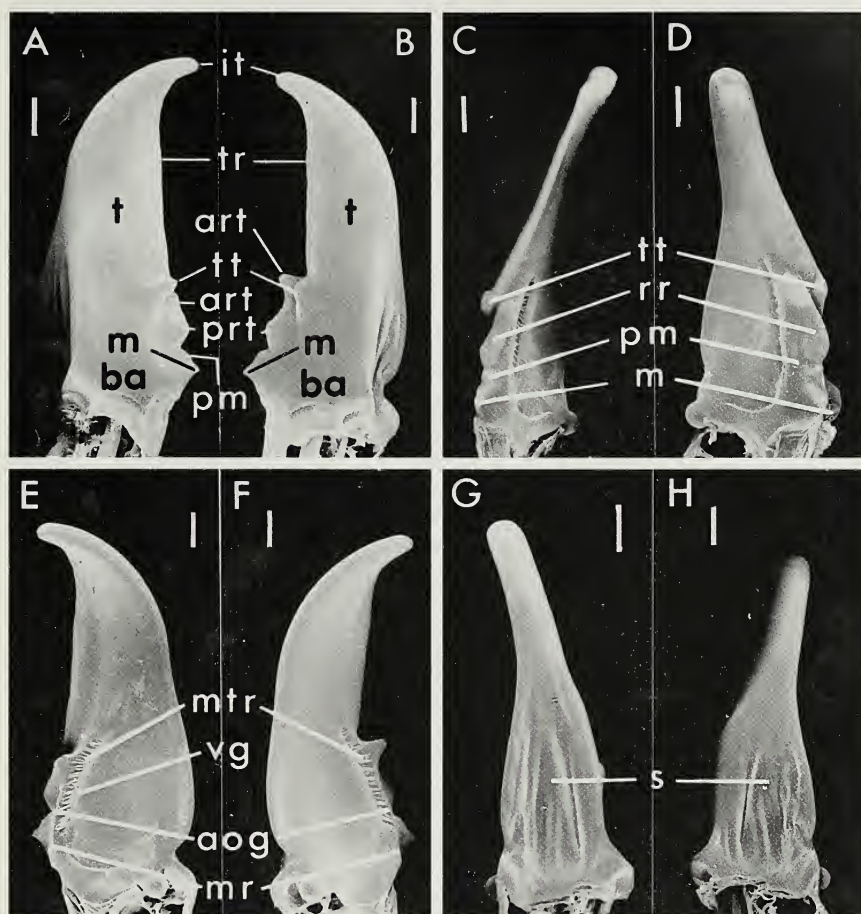


Fig. 5.—SEM photographs of mandibles of *Rawlinsius papillatus*, n. gen., n. sp. A, C, E, G, left mandible, dorsal, occlusal, ventral, and lateral aspects, respectively. B, D, F, H, right mandible, dorsal, occlusal, ventral, and lateral aspects, respectively. Abbreviations: aog, anterior occlusal groove; art, anterior retinacular tooth; ba, basal area; it, incisor tooth; m, molar tooth; mr, ventral molar ridge; mtr, microtrichia of ventral groove; pm, premolar tooth; prt, posterior retinacular tooth; rr, retinacular ridge; s, scrobe; t, terebra; tr, terebral ridge; tt, terebral tooth; and vg, ventral groove. Scale bars = 200 μ m.

corresponding to the respective somites. The first complete sternum is III, and the last one (pregenital) normally exposed is VII. For numbering the somites associated with the genitalia, we follow Bils (1976).

Portions of appendages are designated by the suffix “-mere,” the prefix depending upon the appendages in question, e.g., antenno-, palpo-, tarso-, etc.

Mandibles

Acorn and Ball (1991) proposed a general system for recognizing and naming elements of the mandibles. The names provided below (Fig. 5) reflect this general system, as applied to the mandibles of *Rawlinsius*.

Labium

The word “ligula” is used for glossae + paraglossae. In turn, the fused, scler-

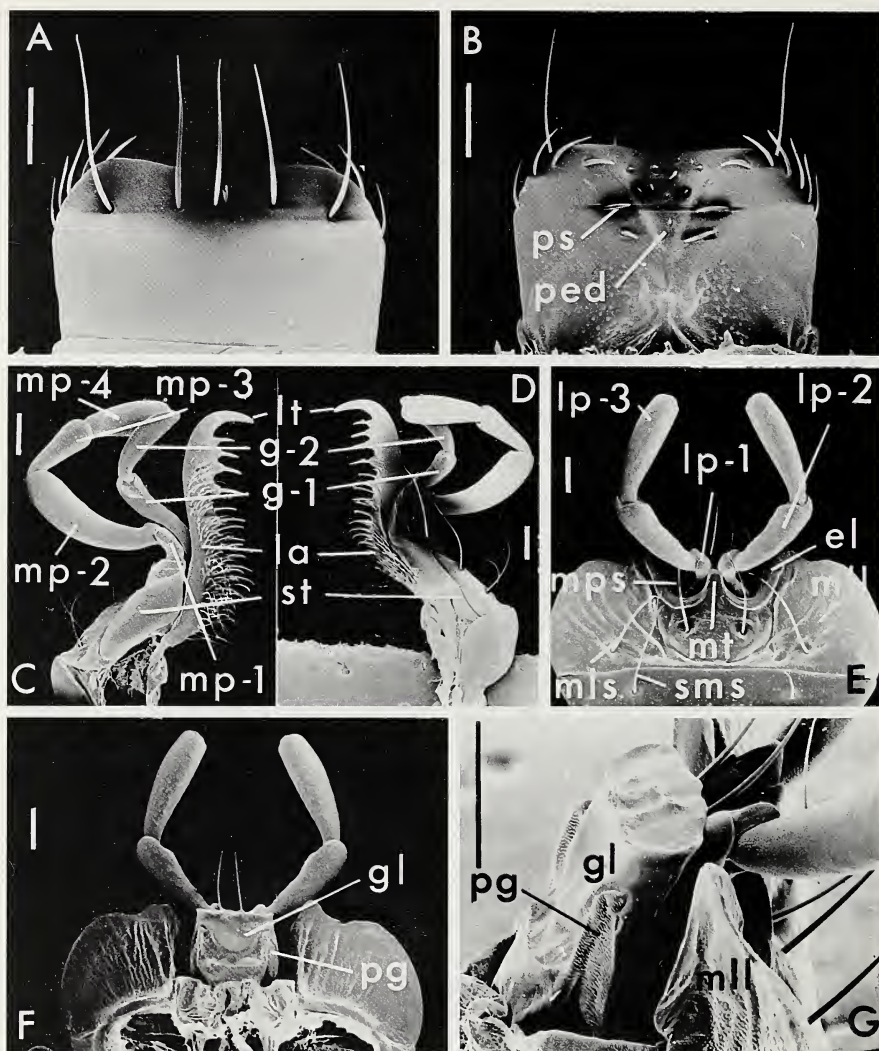


Fig. 6.—SEM photographs of labrum, maxilla, and labium of *Rawlinsius papillatus*, n. gen., n. sp. A, B, labrum, dorsal and ventral aspects, respectively. C, D, left maxilla, dorsal and ventral aspects, respectively. E, F, G, labium: E, F, ventral and dorsal aspects, respectively; G, right lateral aspect of prementum and lateral lobe of mentum. Abbreviations: el, epilobe (mentum); g-1, g-2, galeomeres 1 and 2, respectively; gl, glossal sclerite; la, lacinia; lp-1 to lp-3, labial palpomeres 1–3, respectively; lt, lacinial tooth; mll, mentum, lateral lobe; mp-1–mp-4, maxillary palpomeres 1–4, respectively; mls, mental lateral seta; mps, mental paramedial seta; mt, mental tooth; ped, pedium; pg, paraglossa; ps, parapedial seta; sms, submental seta; and st, stipes. Scale bars = 200 μ m.

otized glossae (Fig. 6F:gl), characteristic of beetles generally, are termed collectively the “glossal sclerite” (Ball and Shpeley, 1983:746).

Elytra

The dorsal surface of the elytra (Fig. 7A) is divided into intervals and striae. Stria is understood to be a collective rather than a descriptive noun, and it encompasses the structures in several character states, not necessarily a grooved or

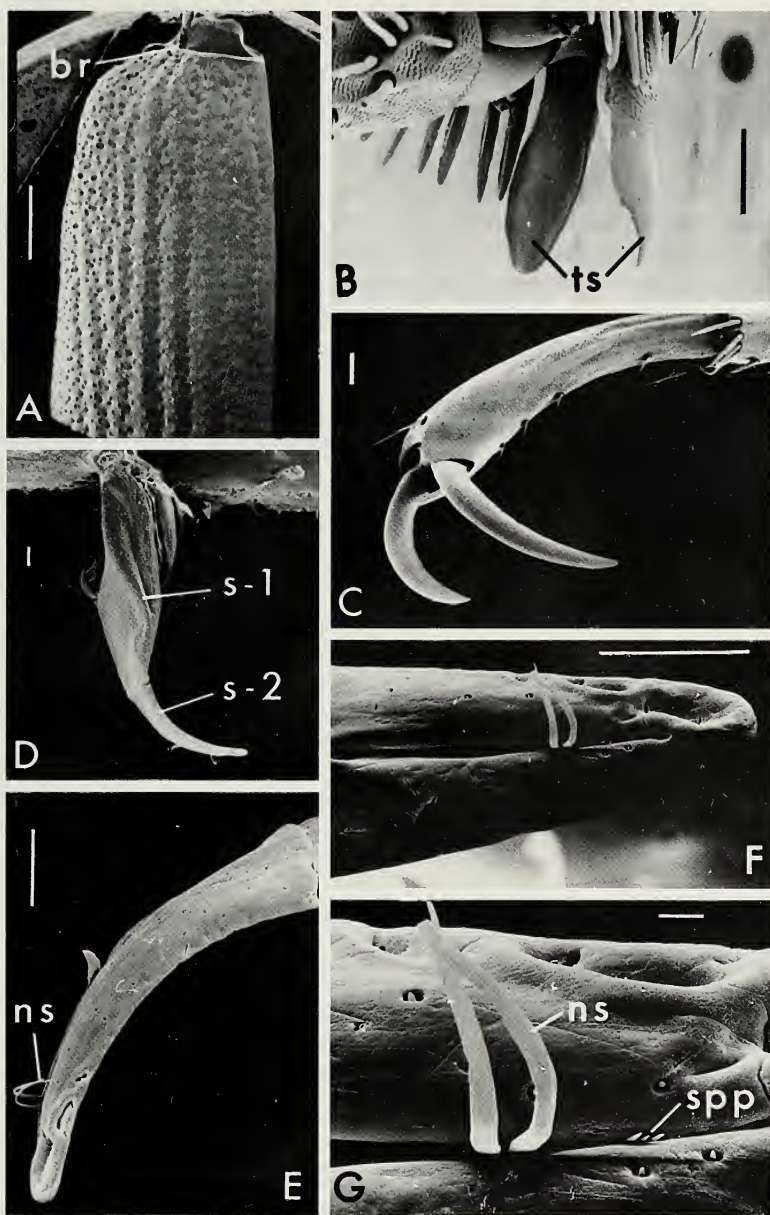


Fig. 7.—SEM photographs of elytra, legs, and ovipositor of *Rawlinsius papillatus*, n. gen., n. sp. A, left elytron, basal portion, dorsal aspect. B, tibial spurs, left hind leg, medial aspect. C, left hind tarsomere 5 and claws, medial aspect. D–G, ovipositor: D, left stylomeres 1 and 2, lateral aspect; E, left stylomere 2, lateral aspect; F, G, stylomere 2, ventral aspect. Abbreviations: br, basal ridge; ns, nematiform seta; s-1 and s-2, stylomeres 1 and 2, respectively; spp, sensory pit peg; ts, tibial spurs. Scale bars: A = 1 mm.; B–F = 100 μ m; G = 10 μ m.

striate character state. A stria can be a complete or abbreviated groove, a series of disconnected grooves or dashes, a row of punctures, or completely absent. The neologism *interneur* (Erwin, 1974:3–5), coined to replace stria, is abandoned due to Cooper's (1990) cogent arguments.

Male Genitalia

The internal sac of members of the subtribe *Broscina* is characterized by a very complex armature (Fig. 10A, B, F–H). To facilitate reference to details, Ball (1956) designated two of the sclerites as *x* and *y*, respectively. There is also an apical plate (*a*), with an extensive and complex field of microtrichia.

Ovipositor

Terms for sclerites of the female genital segments (VIII–X in Coleoptera) and their appendages (Fig. 7D–G, 11A) have a complex history, occasioned principally by different views among authors about homology of the sclerites. Ball and Shpeley (1983:746) explain terms used for sclerites and setae, and orientation of this complex of sclerites. Note that for the stylomeres, the surfaces that are ventral in the infolded position are lateral when the ovipositor is extended; thus, such surfaces are designated as lateral, and the other surfaces are designated accordingly.

We make reference here only to the appendages putatively of segment IX (or IX + X; Bills, 1976), comprising two stylomeres (*s*-1 and *s*-2; Fig. 7D, 11A). Noonan (1973:275) explains the morphological basis for regarding the stylus as bipartite, rather than as “coxite” and “stylus” (Tanner, 1927). Stylomere 2 is referred to by Deuve (1993) as gonopod IX. Also, he refers to the sensory furrow, or pit (Fig. 7F, G) as the subapical setose organ, in which is inserted a pair of relatively long nematiform setae and a varied number of short sensory pit pegs (Fig. 7F, G:ns, spp).

TAXONOMIC TREATMENT

Tribe Broscini, Characters and Relationships

To determine placement of *Rawlinsius papillatus*, the genus and species described below, it is necessary to consider some general matters about broscine carabids. According to Erwin (1985:467–468) and other authors, the postulated relationships of the Broscini are indicated by the following classification.

- Division Melaeniformes
- Subfamily Broscinae
 - Supertribe Melaenitae
 - Tribe Melaenini
 - Tribe Cymbionotini
 - Supertribe Broscitae
 - Tribe Broscini
 - Supertribe Apotomitae
 - Tribe Apotomini

The sister group of the Melaeniformes is the Psydriformes. The derived feature for this complex (i.e., Melaeniformes + Psydriformes = Harpalinae of Horn [1881] and others) is the conjunct middle coxae. The only derived feature for the

Melaeniformes seems to be the pedunculate body, a feature that Lindroth (1961b: 169) suggested might be a synapomorphy for Broscini + Scaritini.

Within the Melaeniformes, most of the supposedly diagnostic features of the tribes prove not to be. Even the elaborate sclerotization of the internal sac of the subtribe Broscina is shared with at least the melaenines and cymbionotines, but not with the Apotomini, males of which lack complex armature. As well, this complex armature occurs in males of the seemingly unrelated pausoid complex and the Elaphrini. Goulet (1983:460), however, concluded that, based on structural details of the male genitalia, the tribe Elaphrini probably was related to the subtribe Broscina and to the tribe Melaenini.

Evidence for including *Rawlinsius papillatus* in the tribe Broscini is based on the following combination of diagnostic features: integument glabrous, without vestiture of short setae; prothoracic–mesothoracic junction pedunculate, with scutellum short and broad and located anteriorly to the elytral humeri; head with occiput with a transverse groove; mouthparts as described below, especially the bisetose labial palpomere 2 and the toothed mentum; middle coxal cavities conjunct; fore tibia anisochaetous; elytron without discal setae, and with lateral margin posteriorly uninterrupted by a plica; parameres of male genitalia long and setose apically; and ovipositor stylomere 2 without marginal ensiform setae. The armature of the internal sac of the male genitalia (sclerite x with pair of apical flanges—f, Fig. 10B, F, G) is typical of the Northern Hemisphere assemblage of the subtribe Broscina.

With the exception of the flanges on sclerite x of the internal sac, the features recorded above are plesiomorphic within the division Melaeniformes and subfamily Broscinae. Together, however, they define the tribe Broscini (in a formal, if not phylogenetic, sense). More particularly, they define the Northern Hemisphere assemblage of the subtribe Broscina (excluding *Axonya* and *Broscodes*), and their possession prevents inclusion of *Rawlinsius* in any other suprageneric melaeniform taxon.

The following ten genera of Broscina are represented in the New World, grouped (Ball, 1956; Roig Juárez, 1995; Roig Juárez and Ball, 1995) as follows:

Subtribe Baripodina: *Baripus* Dejean 1828 (Argentina, Chile, Uruguay; 22 species);

Subtribe Creobiina: *Cascellius* Curtis 1839 (Argentina, Chile; two species); *Creobius* Guérin-Ménéville 1838 (Argentina, Chile; one species); and *Nothocasellius* Roig Juárez 1995 (Argentina, Chile; two species);

Subtribe Broscina: *Broscodera* Lindroth 1961a (Nearctic; one species); *Broscus* Panzer 1813 (many Palearctic species, one species introduced in the Nearctic); *Miscodera* Eschscholtz 1830 (Holarctic; one species); *Nothobroscus* Roig Juárez and Ball 1995 (Chile; one species); *Rawlinsius*, n. gen. (Mexico; one species); and *Zacotus* LeConte 1869 (Nearctic; one species).

The following key, based on external features of adults, allows identification of the broscine subtribes and genera of the New World.

Key to Subtribes and Genera of Broscini in the New World

(Based in part on Roig Juárez and Ball, 1995:303, and Roig Juárez, 1995:53)

- 1 Eyes emarginate anteriorly; prosternum with pair or cluster of setae at apex of intercoxal process; elytron basally without parascutellar seta; abdominal sterna V–VII each with

- complete transverse groove. Argentina, Chile, Uruguay. (Subtribe Baripodina) *Baripus* Dejean
- 1' Eyes not emarginate, anterior margin evenly rounded in outline; prosternum with apex of intercoxal process asetose; elytron without or with parascutellar seta; abdominal sterna V–VII each with or without transverse groove, smooth or with one or two lateral grooves, each side 2
- 2 (1') Labium with glossal sclerite apically quadrisetose. (Subtribe Creobiina) 3
- 2' Labium with glossal sclerite apically bisetose (Fig. 6E–G). (Subtribe Broscina) 5
- 3 (2) Head with three or more pairs of supraorbital setae; pronotum with more than two pairs (four pairs in most individuals) of lateral marginal setae; abdominal sterna V–VII anteriorly without transverse groove. Argentina, Chile *Creobius* Guérin-Ménéville
- 3' Head with one pair of supraorbital setae; pronotum with two pairs of lateral marginal setae; abdominal sterna V–VII anteriorly with transverse groove 4
- 4 (3') Eyes convex; elytra (in profile) with apex on same plane as epipleura; male with mid tarsomeres 1–3 and fore tarsomeres 1–4 with adhesive vestiture. Argentina, Chile *Cascellius* Curtis
- 4' Eyes flatter; elytra (in profile) with apex downcurved below plane of epipleura; male with fore tarsomeres 1–2 or 1–3 with adhesive vestiture, mid tarsomeres without vestiture. Argentina, Chile *Nothocasellius* Roig Juárez
- 5 (2') Dorsal surface without fixed setae (mandibular scrobal, clypeal, supraorbital, lateral pronotal, elytral–parascutellar, discal, or lateral umbilical); metepisternum longer than wide; elytra with dorsal surfaces papillate; abdominal sterna V–VII with transverse groove close to anterior margin; macropterous. Mexico *Rawlinsius*, new genus
- 5' Dorsal surface with fixed setae (at least clypeal, supraorbital, lateral pronotal, and elytral lateral umbilical); metepisternum longer than wide, or as long as wide at base; elytra with dorsal surfaces smooth, not papillate; abdominal sterna V–VII without transverse groove; macropterous or brachypterous 6
- 6 (5') Labial mentum with tooth bifid at apex and with paramedian pits; elytron without parascutellar seta; dorsal integument black. Chile *Nothobroschus* Roig Juárez and Ball
- 6' Labial mentum (Fig. 6E) with tooth simple at apex, with or without paramedian pits; elytron with parascutellar seta; dorsal integument black or coppery and green. Nearctic or Holarctic 7
- 7 (6') Pronotum with single pair of marginal setae (posterior pair lacking); pronotum markedly constricted posteriorly, with deep transverse groove; mentum with paramedian pits. Northern Holarctic *Miscodera* Eschscholtz
- 7' Pronotum with two pairs of marginal setae; pronotum not markedly constricted posteriorly, without deep posterior groove; mentum with or without paramedian pits 8
- 8 (7') Head with frons and vertex more or less grooved and rugose; mentum without paramedian pits. Nearctic, Pacific Northwest *Zacotus* LeConte
- 8' Head with dorsal surface smooth, except frontal impressions and sparse punctation; mentum with or without paramedian pits 9
- 9 (8') Middle femur with row of about six setae ventrad on anterior surface; tarsomeres 1–4 with dorsal surfaces smooth, glabrous; eight or nine setae in elytral umbilical series; mentum without paramedian pits; overall length of body about 20 mm. Palaearctic; introduced in North America, known only from coastal localities in maritime Canada . . . *Broschus* Panzer
- 9' Middle femur with row of not more than three setae ventrad on anterior face; tarsomeres 1–4 with dorsal surfaces rugulose and sparsely setose; mentum with paramedian pits; three

or four setae in elytral umbilical series; overall length of body about 10 mm. Western North America *Broscodera* Lindroth

Rawlinsius, new genus

Type Species

Rawlinsius papillatus, new species; here designated.

Generic Name

Eponym, masculine, based on the surname of the collector of the first specimen, John E. Rawlins, Carnegie Museum of Natural History. We take great pleasure in naming this new genus after our friend and colleague. His extraordinary perseverance in the field and great breadth of coverage when collecting have led to this and many other fine discoveries.

Recognition of Adults

See key.

Description

None required because the genus is monobasic, and its characters are the same as those of its type species, which is described below.

Larvae

We note here the features that establish the two larvae as members of the tribe Broscini, based on the diagnostic features indicated by Jeannel (1941:288), van Emden (1942:17), and Thompson (1979: 225, 247): head with cervical grooves; antenna with antennomere 1 longest of antennomeres 1–4; outer lobe of maxilla with article 1 longer than 2, inner lobe represented by a stout seta; urogomphus longer than the pygopodium; and each tarsus terminated in a single claw. In Moore's (1964:244) key to the four genera of Broscini with known larvae, the putative *Rawlinsius* larvae exhibit the diagnostic features of *Broscus*, type genus of the subtribe Broscina. Two distinctive features of the *Rawlinsius* larvae are the mandibles with two teeth (a feature shared with Omophronini), and the moderately densely setose integument.

Geographical Distribution

See Figure 12 and under species description below.

Chorological Affinities

The only known locality of this genus is isolated by about 3000 km from the range of other Northern Hemisphere broscines, and by about 7500 km from the range of south temperate New World broscines.

Phylogenetic Relationships

The flanges on sclerite x of the male internal sac (Fig. 10B, F, G:f) represent a putative synapomorphy for a group of Palaearctic and Nearctic members of the subtribe Broscina. Because males of *Rawlinsius* have these flanges, we postulate that the genus is a member of this northern assemblage of the subtribe Broscina. Within this assemblage (Northern Hemisphere Broscina, excluding *Axonya* Andrewes and *Broscodes* Bolivar), *Rawlinsius* is distinctive in the following features of the male genitalia: basal bulb open widely, opening extended onto dorsal surface; and sclerite x of the internal sac neither markedly constricted basally nor terminated in a short subuliform projection (Roig Juñent, personal communication). If these genitalic features of *Rawlinsius* prove plesiomorphic, this genus may be the adelphotaxon to the other northern broscine genera, with exclusions as noted above.

Rawlinsius papillatus, new species

Type Material

Holotype male, labelled: "MEXICO: Guerrero/ 26 km NW El Paraiso/ 1800 m.

8 Aug 1986/ R. Davidson, J. Rawlins". Paratypes 12, with five males and six females labelled as holotype. One female labelled same as holotype, except: "July 3, 1982, J. Rawlins". Holotype and ten paratypes at Carnegie Museum of Natural History; one male paratype deposited at University of Alberta, Strickland Museum; one female paratype deposited at Departamento de Zoología, Instituto de Biología, Universidad Nacional Autónoma de México.

Type Locality

The locality indicated above for the type series, more specifically, is at 17°29'N, 100°12'W in the Sierra de Atoyac de Alvarez section of the Sierra Madre del Sur, Guerrero, Mexico. This is according to the Carta de México Topográfica 1: 250,000 (Anonymous, 1982). The road had been washed out and rebuilt in places in a different direction, and several maps examined each showed the trend of the road in a different orientation from El Paraiso (NW, N, NNE). Without a Global Positioning System device, it was impossible to be certain of the exact latitude and longitude or general direction. Nonetheless, there is only one road from Atoyac through El Paraiso, continuing over the summit just below Cerro Teotepec, and dropping down the east face to Filo de Caballo and Xochipala. The exact straight-line distance from El Paraiso to the type locality is not known. Traveling approximately 26 km from El Paraiso along the road to Cerro Teotepec will take the interested collector to the proper site. The detailed description of habitat in the present paper should allow one to recognize the microsite. Vargas-Fernandez et al. (1992:46–55) provide a good description of the region, an illustration (fig. 3, p. 51) of the drainage system, an interpretation of the position of the road, and an illustration (fig. 6, p. 55) of the vegetation profile.

Specific Epithet

A Latin masculine adjective, referring to the papillate dorsal surface of the elytra (Fig. 4A, C).

Recognition

Adults are rather large carabids (overall length 15–20 mm), with dark integument that is metallic blue-green when wet (Fig. 3A, B). The dorsal surface is devoid of setae, including the standard fixed setae: clypeal and supraorbital of the head; antennal scape, apex of pedicel, and antennomere 3; lateral pronotal; and parascutellar, discal, and lateral umbilical of the elytra. Lacking also are the scrobal setae of the mandibles, the presence of which is a ground-plan feature of the tribe Broscini.

Description

Habitus as in Figures 1, 2, 3A, B. Attitude partly hypognathous. Overall length of body, males, 15–18 mm (mean 16.9 mm); females, 18–20 mm (mean 19.1 mm). Maximum width (elytra), males, 5.5–6.0 mm (mean 5.7 mm); females, 6–7 mm (mean 6.4 mm). Surface glabrous.

Color and Luster.—Dorsal surface when dry predominantly black, tinged with metallic blue-green to purple (color especially evident on surface viewed obliquely); dorsal surface when wet predominantly bright metallic blue-green (Fig. 3A, B). Ventral surface, mouthparts (including palpi), and legs dark piceous to black. Setae of tibiae, tarsi, mentum, and labrum yellow-brown. Dorsal surface rather dull when dry; shiny when wet.

Microsculpture.—Dorsal surface granulate, with mesh pattern predominantly approximately isodiametric, sculpticells slightly elongate (Fig. 4B); sculpticells small, each with surface slightly convex. Ventral surface with mesh pattern more transverse, sculpticells with surface flat.

Macrosculpture.—Head with clypeus, frons, and vertex rather coarsely, moderately densely punctate, occiput more sparsely punctate or impunctate; frons and vertex laterally grooved and ridged vermiculately. Ventral surface with genae and postgenae moderately densely, coarsely punctate; gula smooth. Pronotum coarsely, densely punctate anteriorly, laterally, and posteriorly; disc centrally ru-

gulate, with rather prominent transverse rugulae. Proepipleura shallowly to deeply punctate. Propleura and prosternum punctate and vermiculately rugulose. Pterothoracic pleura, lateral areas of sterna, and lateral areas of hind coxae coarsely and sparsely punctate, central parts of sterna smooth. Elytral surface irregular, with numerous small papillate swellings (Fig. 4A, C–E) mainly in longitudinal rows centrally on intervals (Fig. 4A), but not confined to such position. Striae with coarse irregular punctures. Elytral epipleura with short row of dashlike punctures near humeri.

Head.—More or less quadrate in outline. Dorsally, clypeus somewhat swollen posteriorly; frontal impressions indistinctly delimited, basinlike; occiput grooved shallowly, transversely; postocular areas inflated. Laterally, paragenae broad anteriorly, tapered beneath eye to slightly narrower than width of antennal scape. Eyes moderate in size, slightly convex. Antennae filiform; antennomeres 1 (scape)—4 glabrous with apical fixed setae only on 4; antennomeres 5–10 with dense covering of short sensory setae and apical fixed setae present; scape rather thick; pedicel short; antennomere 3 elongate, about 1.25 length of antennomere 5; antennomeres 4–11 as in most *Broschini*.

Labrum.—Labrum (Fig. 6A, B) rectangular, transverse; dorsal surface (Fig. 6A) with six long setae, inserted preapically in five punctures, middle pair sharing same puncture. Ventral surface with epipharynx (Fig. 6B) very simple, reduced markedly, pedium (ped) short, narrowly triangular, with few peglike sensilla; parapedal setae (ps) few; crepis and parapedal projection not evident.

Mandibles.—Mandibles (Fig. 5A–H) trigonal in outline, slightly curved ventrally; scrobes grooved, without scrobal seta apically (Fig. 5G, H). Left mandible (Fig. 5A, C, E, G) in dorsal aspect (Fig. 5A) with short incisor tooth (it), rounded apically; terebra (t) long, occlusal surface with supraterebral ridge indistinct, terebral ridge (tr) nearly straight, curved slightly; retinaculum short, anterior and posterior retinacular teeth (art, prt) indistinct, blunt apically; and molar tooth (m) short; occlusal surface (Fig. 5C) with posterior occlusal groove absent; ventral surface (Fig. 5E) with molar ridge (mr) short and with ventral groove (vg) short, about one-third length of mandible; microtrichia (mtr) relatively sparse. Right mandible (Fig. 5B, D, F, H) similar to left, except: terebra narrower; terebral tooth smaller; retinaculum with anterior and posterior teeth more prominent, retinacular ridge (rr) concave; and molar tooth more prominent.

Maxillae.—Maxillae (Fig. 6C, D) with stipes (st) with three lateral setae. Lacinia (la) with apical tooth (lt) thick, markedly curved mediad in relation to long axis of lacinia; occlusal surface with four prominent, thick spines in apical half; basal half with row of relatively large, curved setae; dorsal surface with sparse vestiture of smaller setae. Galeomeres 1 and 2 (g-1, g-2) subequal in length. Palpomeres 3 and 4 (mp-3, mp-4) subequal in length, each about one-half length of palpomere 2 (mp-2); palpomere 1 (mp-1) about one-third length of palpomere 2.

Labium.—Labium (Fig. 6E–G), ventral aspect (Fig. 6E). Submentum with single pair of setae (sms); mentum with two pairs of setae, one pair paramedial (mps), and one pair more lateral (mls). Mentum transverse, anteriorly with broad sinus and prominent medial tooth (mt); lateral lobes (ml) broad, each broadly rounded laterally, apical margin sinuate; epilobes (el) clearly marked throughout length. Ligula with glossal sclerite (gl) bisetose apically, rather broad and thick (Fig. 6F, G), apical margin subtruncate; paraglossae not visible; dorsal surface (Fig. 6F) with paraglossae (pg) evident, each with vestiture of numerous short microtrichia. Palpomere 2 (lp-2) bisetose; palpomeres 2 and 3 (lp-2, lp-3) subequal in length; palpomere 1 (lp-1) about one-fifth length of palpomere 2.

Prothorax.—Pronotum rather narrow, with length and width subequal, but wider than head across eyes, and base distinctly wider than apex; anterior (apical) margin slightly concave; posterior margin slightly lobed medially; lateral margins rounded anteriorly, sinuate posteriorly, epipleuron visible in sinuation from dorsal aspect; anteriolateral angles rounded narrowly, not projected forward; posteriolateral angles about rectangular, but narrowly rounded; anterior and posterior margins not beaded; anterior and posterior transverse impressions barely indicated, median longitudinal impression distinct in middle part of pronotum; anterior surface generally convex, slightly flattened dorsally, without lateral grooves and surface rounded evenly each side to epipleural margin. Prosternum with intercoxal process not margined apically.

Pterothorax.—Metepisternum very long and narrow; metepimeron narrow, truncate posteriorly.

Scutellum.—Short, broad, rounded posteriorly; mostly concealed beneath posterior margin of pronotum.

Elytra.—Long and slender, depressed antieriad basal ridge (Fig. 7A:br). Basal ridge thick laterally, to level of interval 6, extended to suture as thin line not elevated above surface posteriorly; apical margin complete, not interrupted laterally by plica; apical declivity sloped ventrally slightly and gradually. Striae (Fig. 4A:in) broad, shallow, indistinctly delimited; parascutellar stria evident. Intervals (Fig. 4A:it) slightly convex.

Wings.—Fully developed (Fig. 8); venation as in most *Carabidae*; oblongum cell (o) large; wedge cell (w) small.

Legs.—Long and slender (Fig. 9A); hind leg, length trochanter/length femur 0.19; dorsal surface of

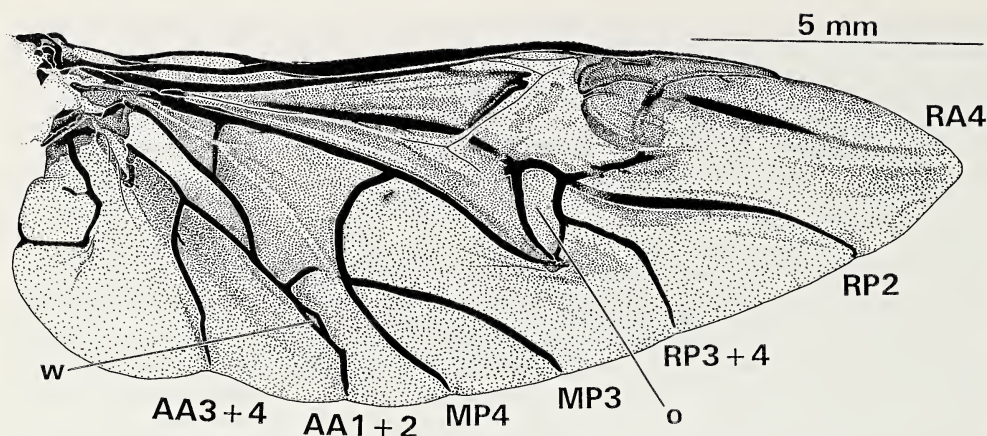


Fig. 8.—Right hind wing of *Rawlinsius papillatus*, n. gen., n. sp., dorsal aspect. Abbreviations: AA 1 + 2, anterior anal vein 1 + 2; AA 3 + 4, anterior anal vein 3 + 4; MP 3, posterior medial vein 3; MP 4, posterior medial vein 4; o, oblongum cell; RA 4, anterior radial vein 4; RP 2, posterior radial vein 2; RP 3 + 4, posterior radial vein 3 + 4; w, wedge cell.

femora with small tubercles, these evanescent on other faces; middle femur with few setae proximally; anterior surface of front tibia, most of middle and hind tibiae, and dorsal surfaces of tarsomeres rugulose (Fig. 7C); proximal half of tibiae, especially middle and hind tibiae, with three indistinct carinae; tibiae with longitudinal rows of spines in apical third only, spines thin; middle tibia without apical cleaning brush; tibial spurs (Fig. 7B:ts) spatulate. Tarsomeres 1–4 each with many stiff setae laterally, ventrally, and apically; tarsomere 5 (Fig. 7C) elongate, longer than tarsomeres 2–4, ventrally with row of setae on lateral margins; tarsal claws average size for broscines of this length, curved; unguitractor plate broad, flat, rounded at apex. Male fore and middle tarsomeres without adhesive vestiture ventrally.

Abdominal Sterna.—As in most Carabidae, but ambulatory setae absent from sterna IV, V, and VI; sternum VII with single pair of setae preapically; sterna III and IV laterally with surfaces depressed, depressions occupied by basal parts of legs; sterna V–VII each near anterior margin with deep transverse groove. Sternum VII of male (Fig. 9B) very broadly rounded apically, female (Fig. 9C) much more narrowly and abruptly rounded.

Male Genitalia.—Median lobe (Fig. 10A, B:ml) as in most Broscina: basal opening wide, extended onto dorsal surface, margins nearly truncate in lateral aspect; dorsal membrane extensive; apical portion in ventral aspect tapered to a narrow point (Fig. 10C). Internal sac (Fig. 10A, B, F–H) with sclerites x and y, and apical plate (a) (Ball, 1956:48, fig. 3) with large and complex microtrichial field (Fig. 10F–H); gonopore (go) positioned as in Fig. 10H in complex folds at apex of sac; sclerite x basally not constricted, and with pair of flanges extended apically; apically, in dorsal aspect, tapered evenly to blunt point, neither constricted abruptly, nor terminated in subuliform projection (Fig. 10F, G:x, f). Parameres (Fig. 10D, E) long, left styliiform (Fig. 10A, B, D:lp), basally broader than right, each tapered apically, and each setose in apical third.

Spermatophore.—Elongate and irregular (Fig. 11B, C:spa), shaped as in Figure 11B and apparently attached near spermathecal opening.

Ovipositor.—Stylomere 2 shorter than stylomere 1 (Fig. 7D, 11A:s-1, s-2). Stylomere 1 with several setae apically, on medial side. Stylomere 2 (Fig. 7E, F) with apex tapered to bluntly rounded tip; margins without ensiform setae; ventral surface (Fig. 7F, G) with sensory pit long, narrow, with two short nematiform setae (ns) and several pit pegs (spp). Ramus lacking mesad stylomere 1.

Internal Reproductive Organs, Female.—Reproductive tract (Fig. 11A, C) with bursa copulatrix (bc) elongate, with long spermathecal gland (sg); spermatheca (sp) moderately long, at base with helminthoid bursal sclerite (hsc). Spermatheca and spermathecal gland entering bursa separately.

Note on Presumed Spermatophore

The structure illustrated in Fig. 11B was removed from the bursa copulatrix of a female. We assume it to be a spermatophore. Little is known about spermatophore

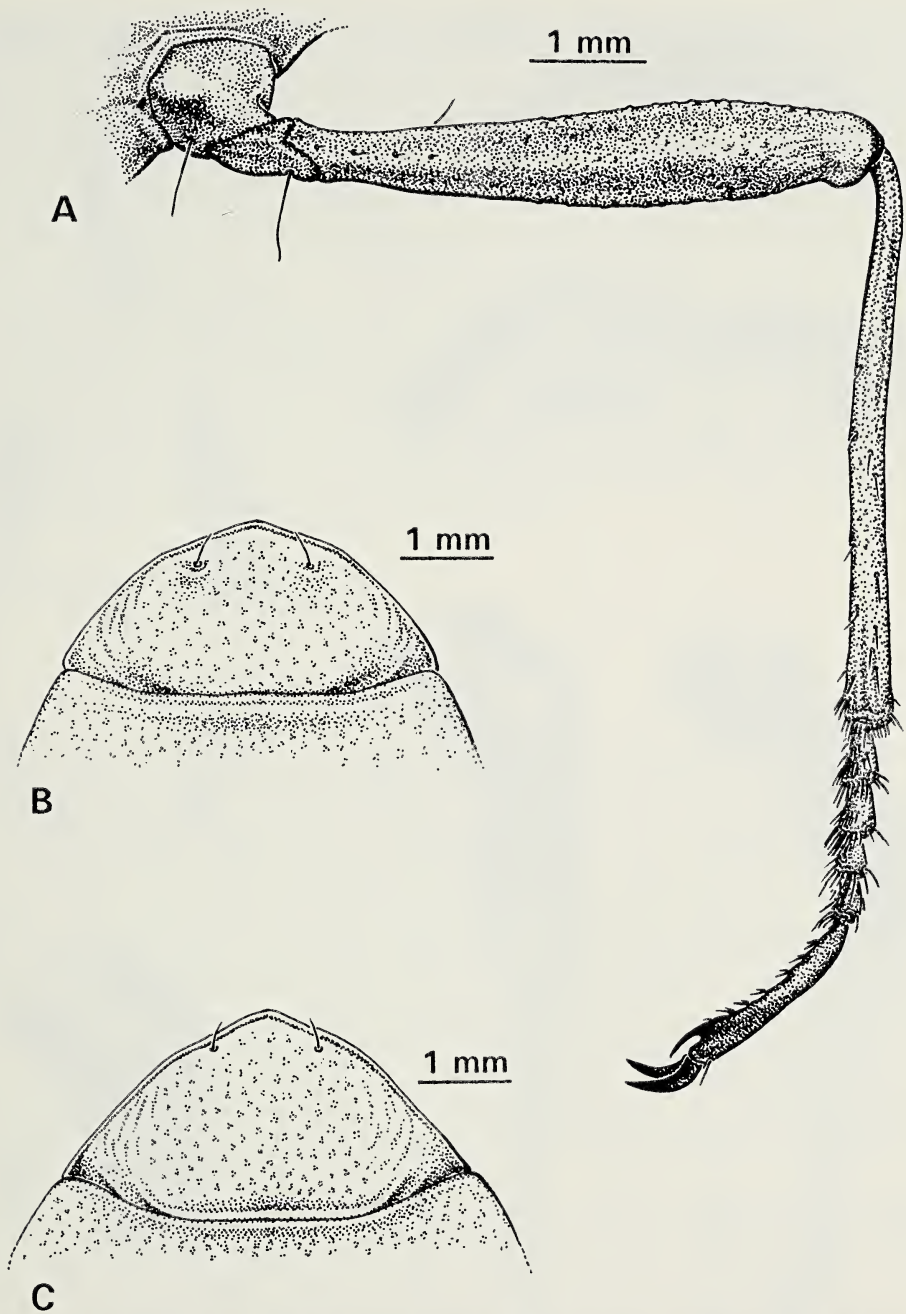


Fig. 9.—Line drawings of leg and abdominal sternum VII of *Rawlinsius papillatus*, n. gen., n. sp. A, left middle leg, anterior aspect. B, abdominal sternum VII of male, ventral aspect. C, abdominal sternum VII, female, ventral aspect.

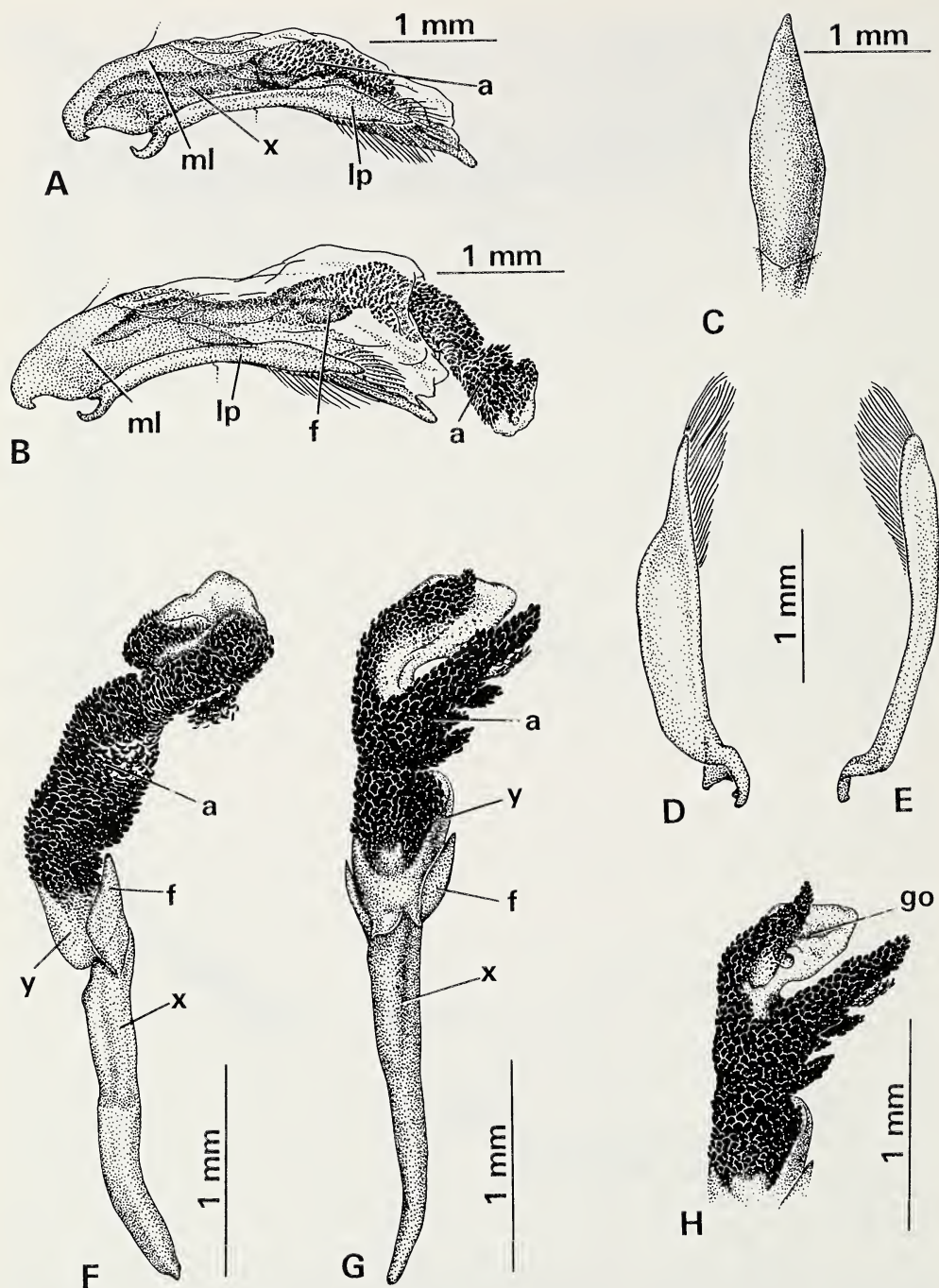


Fig. 10.—Line drawings of male genitalia of *Rawlinsius papillatus*, n. gen., n. sp. A, median lobe and armature of internal sac completely inverted, left lateral aspect. B, same, but internal sac partially everted. C, median lobe, apical portion, ventral aspect. D, E, left and right parameres, respectively, ventral aspect. F, G, H, armature of internal sac, everted: F, left lateral aspect; G, dorsal aspect; H, apical portion, left lateral aspect. Abbreviations: a, apical plate, showing microtrichial field; f, lateral flange of sclerite x; go, gonopore; lp, left paramere; ml, median lobe; x, y, sclerites of internal sac.

phores in Carabidae. Crowson (1981:401) asserted that, in Coleoptera, the most common mode of sperm transmission is "in the form of packets or spermatophores." Jeannel (1928:356–357, footnote 1) discussed the evolutionary significance of spermatophores generally, and illustrated one (fig. 1725) for a species of trechine carabid. He stated that finding a spermatophore was a rare event, and that he had seen only one in the numerous dissections of carabid males that he had made. We examined the bursae of two other female *Rawlinsius*. They each contained a transparent bag, probably the remnants of spent spermatophores.

Geographical Distribution

Known only from the type locality (Fig. 12), in Guerrero, Mexico, the species is expected to occur in suitable habitat throughout at least the south face of the Sierra de Atoyac de Alvarez and probably throughout the Sierra Madre del Sur in Guerrero and into Oaxaca. It or a related species might also be in Guatemala. The species *Hyperthaema sororita* Schaus (Lepidoptera: Arctiidae), thought to be precinctive to Guatemala (J. E. Rawlins, personal communication), was taken at the broscine site during both trips (1981, 1986).

Phylogenetic Relationships

See topic under generic treatment.

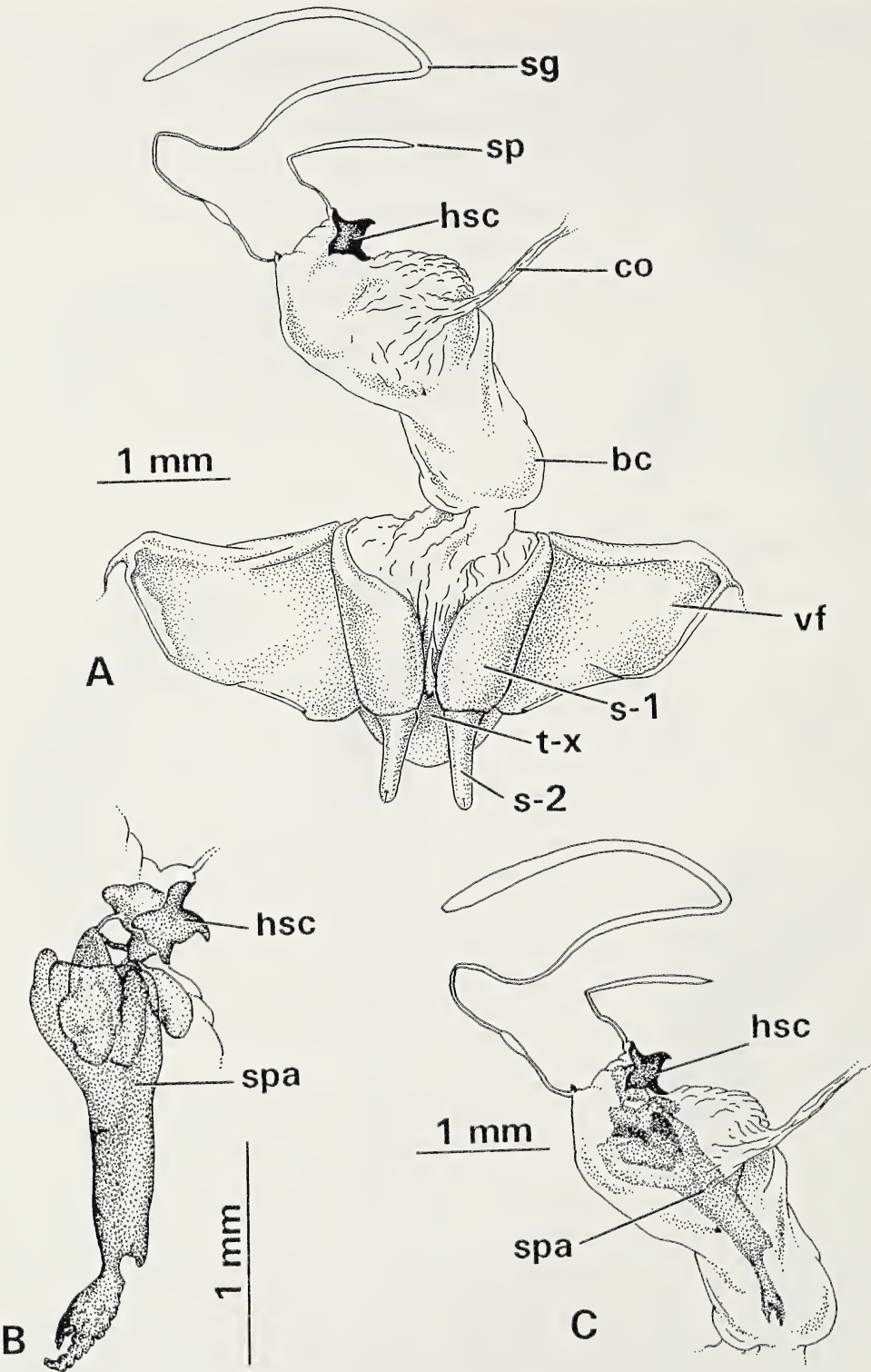
NATURAL HISTORY

Habitat

The beetles were taken in the overflow of a small stream that flowed down a steep gradient off the mountain until it intersected a road cut which formed a cliff about 3 m high. At the road cut, the main channel formed a small waterfall jetting on to the road, and the water then flowed across the road and down the cliff on the downhill side. The steep gradient did not allow access to the stream except where it flowed over the 3-m cliff on the uphill side of the road. In this area, the edges of the stream formed thin sheets of running water at the crest of the cliff and along the vertical rock face to the sides of the waterfall. Three adults and one larva were found in this area, near the top of the cliff. A small finger of water, segregated from the main stream above the cliff, spread into a thin sheet of fast-running water. This flowed down the vertical rock face about 4 m to the left (viewed facing uphill) of the main channel, forming a thin vertical sheet of fast-running water about a meter wide and 3 m high (Fig. 3C). The lush growth of mosses and algae in this flow suggest it is relatively permanent. Ten adults and one larva were found in this tiny area.

The nature of the terrain and the equipment at hand did not permit sampling above or below the road cut. It was impossible to determine whether beetles occurred only on the vertical wet faces or might also be present in shallow water along the steep gradient (where much water flowed in thin sheets across bare rock) or the occasional flat benches visible above. The stream above flowed in thin sheets down several vertical faces and steep slopes, any of which might have been suitable habitat. No beetles were found in the deeper water of the main channel, but this too was accessible only at the crest of the roadside cliff. It was impossible to check the main channel in flatter places above.

Three other streams along the same road (two near the same altitude, one a few hundred meters lower) were searched unsuccessfully for these beetles, both



during the day and at night. Two of the streams were quite different in character, flowing under dense vegetation or with more typical boulder outcrops and sandy or gravelly bottoms and banks. The third stream was similar to the broscine stream in some respects as it flowed over sloping bare rock in places, but it lacked the vertical faces and the thin sheets of flowing water. The apparent absence of *R. papillatus* in these streams suggests that the beetles are very particular about microhabitat.

Voucher specimens were taken of plants growing in the small patch of water where most of the beetles were collected. The dominant plants were several mosses (including *Anomobryum plicatum* Card. [Bryaceae] and *Breutelia* sp. [Bartramiaceae]), a species of *Selaginella* (Selaginellaceae), *Pilea* sp. (Urticaceae), *Campylongus oblongus* (Dicranaceae), and an undetermined sedge (Cyperaceae) (voucher specimens in Carnegie Museum Herbarium, *Rawlins & Davidson* 285 to 290). These are all plants characteristic of permanently wet microsites. A hydrophilid beetle (*Cymbiodyta brevipalpus* Smetana) was also common in the same microhabitat.

The general surrounding habitat was Lower Cloud Forest typical of the Sierra de Atoyac de Alvarez at middle altitudes. The area has been described in some detail by Vargas-Fernandez et al. (1992).

Behavior

These beetles forage, feed, and mate at night in shallow sheets of running water on sheer rock faces. Adults, active in the water after dark, were not found in the daytime, probably having retreated into deep crevices in the surrounding rock. It is unlikely that they spend the day in the water or even very close to the water. Davidson and Rawlins studied several individuals (Fig. 3A, B) at night in their natural habitat and in captivity during the day.

In the first observations (just after dark) of these beetles in 1986, seven or eight individuals were fairly evenly distributed over the main part of the small area of habitat. Exposed to the lights, many of them began to move toward the edges and into the darkness and vegetation. Removal of the lights for a time permitted them to settle, and keeping them in the dimmer edge of the beam allowed most of the observations discussed below without apparent disturbance.

The beetles moved in two very different manners. Most of them remained under water most of the time. They bent the legs such that the venter of the body was pressed flat against the rock, and the water running over their backs helped keep them appressed against the substrate. In this position, they moved very quickly under the water like tiny submarines. They moved upstream, downstream, and cross-current with equal ease, as far as the observers could tell. Several individuals poked their heads into clumps of moss or algae as if searching for food, and on at least two occasions beetles seemed to be capturing something. The observers

←

Fig. 11.—Line drawings, ventral aspect, of ovipositor and internal reproductive organs of female, and male spermatophore, of *Rawlinsius papillatus*, n. gen., n. sp. A, bursa copulatrix and associated structures, ventral aspect, $\times 25$. B, spermatophore of male, ventral aspect. C, bursa copulatrix with spermatophore, ventral aspect. Abbreviations: sg, spermathecal gland of bursa copulatrix; bc, bursa copulatrix; co, common oviduct; s-1, s-2, ovipositor, stylomeres 1 and 2, respectively; hsc, helminthoid sclerite at base of spermatheca; sp, spermatheca; spa, spermatophore; t-x, tergum X; vf, valvifer.

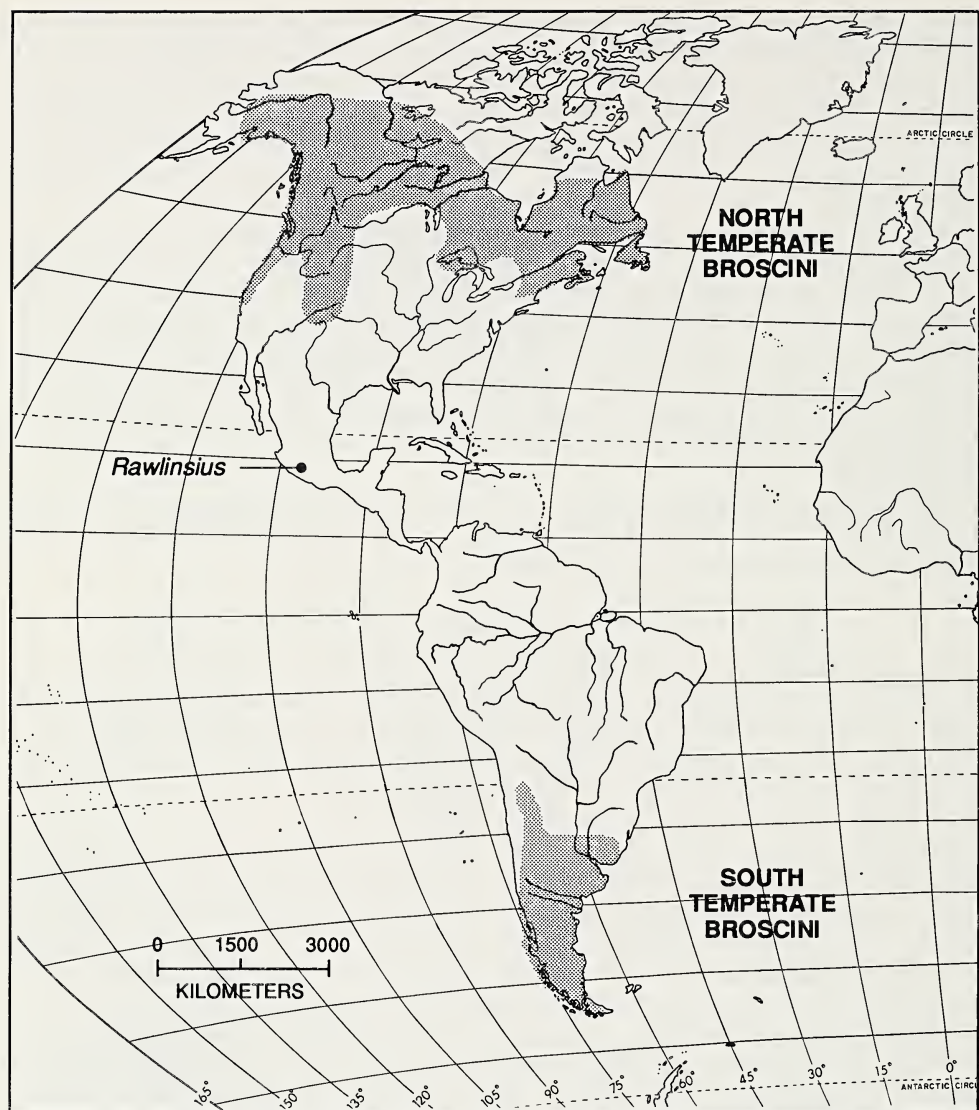


Fig. 12.—Generalized geographical range of the tribe Broscini in the Western Hemisphere.

could not see what the beetles were capturing, but it was most probably tiny Diptera larvae, nematodes, or some other soft invertebrates.

Three individuals used a second manner of locomotion, wading through the water with their bodies above the current, much like a wading bird. The water was so shallow it came only to the middle of the tibiae when the beetles stood up. These individuals stepped quickly through the water, and two individuals thrust their heads under water into clumps of vegetation, presumably searching for food.

Two larvae also were observed briefly. Their movement was quite different from that of the adults. They did not submerge themselves but ran quickly through

the water and several times completely out of the water over the surface of the mosses. Their movement was very frenetic and erratic, faster than the adults, with frequent shifts of direction and frequent plunging of the mandibles and head into vegetation, both above and below water. Foraging on above-water mosses, most of a larva would sometimes disappear into the vegetation. Adult movement, although fast, was much more deliberate, steady, and relatively one-directional.

Two pairs of adults were observed in copulation in the water. One pair was not tightly coupled and broke apart within a few seconds of exposure to the headlamps. The second pair remained coupled, the female under water against the rock, the male on top. Most of the male was above the water surface, as the water was too shallow for both individuals to be submerged.

A few individuals were placed alive in small plastic containers with moss, sand, and rock, on the surfaces of which the beetles moved freely. On several occasions, they lifted the elytra, flexed the flight wings, and tried to fly, colliding with the lid of the container. Adults are clearly capable of flight and must at times disperse up and down the stream or search for other suitable streams. They must do this, however, only at certain times or under certain conditions. An ultraviolet light trap, operated for two nights within 2 m of the habitat, did not attract any of these beetles. This suggests they may not come to ultraviolet light or may do so only when they are prone to flight. It is not known whether flight is frequent and routine, seasonal, weather dependent, or habitat dependent (e.g., lowering stream water level or shifting of stream course).

EVOLUTIONARY ASPECTS

Adaptations

The loss of virtually all normal dorsal setae, presence of which is characteristic of Carabidae, is undoubtedly an adaptation to the unique habitat of *R. papillatus*. Many carabids (e.g., Oodini, Chlaeniini, various Palaearctic species of *Carabus* Linnaeus [Thiele, 1977:218–220]) are active under standing water of swamps, bogs, and wetlands. Several species specialize in splash zones of rapids and waterfalls (e.g., some *Platynus* Bonelli, *Bembidion rufotinctum* Chaudoir, *Pterostichus johnsoni* Ulke). All of these have setation normal for their tribes. Adults of the western North American nebriine, *Nebria ingens* Horn, walk on the substrate underwater in fast-flowing streams and exhibit adaptations in the form of tarsal shape and reduced ventral vestiture (Kavanaugh, 1978). Like *Nebria ingens*, *Rawlinsius papillatus* actively forage under fast-moving water but seem more highly specialized for that role. The only other broscine known to us that seems to be associated with aquatic habitats is *Axonya championi* Andrewes, an Indian species. In his original description, Andrewes (1923:681) refers to a letter from Champion as follows: "Common on river banks in wet places. Runs freely on the water." We cannot tell from this brief remark exactly how aquatic *Axonya* might be.

The tarsal claws (Fig. 7C) seemed to be disproportionately large, much like the tarsal claws characteristic of adult elmids. Measurement of the claws of other broscines proved that *R. papillatus* claws are of average size for a broscine of that length, but the very slender and much elongated legs give the impression of larger claws. Most broscines have robust, stout, relatively short legs. The long, thin legs (Fig. 9A) of *R. papillatus* present less surface resistance to running water, allow the beetle to press its ventral surface against the rock for movement under

water, and allow it to stand upright as if on stilts to wade with its body above the water. Maintaining the claw size when the legs (evolutionarily) have been thinned and elongated leaves a relatively large claw for clinging to rock, and probably the numerous stiff bristles on the ventral side of tarsomeres 1–4 help with movement and attachment. The claws are curved, which no doubt helps the beetle cling to the rock.

The surface of the elytra with extraordinary microsculpture and nipplelike bumps (each with a tiny seta; Fig. 4A–E) is unique in Carabidae so far as we know. The cuticle wets easily and retains a film of water that engulfs the body completely. Most broscine males have some protarsal adhesive vestiture (and some species have some mesotarsal vestiture as well), although markedly reduced in some taxa (e.g., *Nothocascellius hyadesii* [Fairmaire], with only a tiny patch each on protarsomeres 1 and 2 [Roig Juárez, 1995]). Male adhesive vestiture of the protarsi is lost entirely in *R. papillatus*, possibly for the same reasons the dorsal setae are lost, or possibly because the protarsal pads do not function well in gripping the female while mating under water.

The structure of the mouthparts does not indicate external digestion. The mandibles have a short ventral groove (Fig. 5E:vg) and are equipped with short and relatively few microtrichia. The maxillary laciniae (Fig. 6C:la) have long, stiff setae and lack a dense brush of setae, and the epipharynx (Fig. 6B) is reduced. If the beetles feed primarily or at least frequently under running water, external digestion is probably impossible, and the mouthparts certainly suggest that digestion is internal.

The macropterous condition, including body proportions indicative of flying ability (relatively small fore body and hind body with long elytra and large metathorax), is a retained plesiomorphy, with flight being essential for beetles that live in intrinsically unstable riparian habitats.

The adaptive significance of some structures of the female genitalia is not clear, but they will be important in understanding broscine relationships. We therefore discuss briefly three of these structures. In the higher Carabidae (e.g., tribes Pterostichini, Platynini, Oodini, Chlaeniini, Lebiini), the spermatheca and spermathecal gland are joined before their common entry into the bursa. In broscine genera studied (see Deuve, 1993:153–156), including *Rawlinsius*, the spermathecal gland (when present) and the spermatheca enter the bursa separately. This may be the ground plan of the Broscini. Another structure, the ramus (see Bills, 1976, for definition of this term), is plesiomorphically present mesad stylomere 1 (Liebherr and Will, in press). Liebherr and Will found rami in species of *Broscus* and *Zacotus*, and Deuve (1993:154, fig. 235, 237) shows rami in *Broscus* and *Metaglymma* Bates. Deuve (1993:154–155, fig. 238, 239, 241, 242) shows no rami in *Percosoma* Schaum, *Cascellius*, *Broscosoma* Rosenhauer, or *Miscodera*. No doubt substantial dissection is required to determine how this influences broscine relationships. It is important to note that *Rawlinsius* lacks such structures, and that this is synapomorphic within the tribe.

Phylogenetic Interpretation of Adaptive Features

Absence of setae, presence of elytral papillae, and long, slender legs are interpreted as apomorphic features, developed as adaptations for life in close association with running water. Perhaps ancestral broscines were associated with riparian situations, as is *Axonya championi* Andrewes (Andrewes, 1923), and perhaps

Rawlinsius is a survivor of an ancestral riparian lineage. This would fit with the Darlington–Erwin concept of taxon pulses, in which new carabid lineages (specifically) evolved initially in “equatorial wetlands” (Erwin, 1985:462; see also p. 445, fig. 2) and sequentially came to occupy other habitats and other parts of the world, eventually with the primitive riparian lineages becoming extinct in the face of competition from later-evolving and more successful groups. *Rawlinsius* managed to survive in the ancestral zone by evolving to occupy a very special and restricted part of it; it has, so to speak, retained its hold on the central zone of carabid evolution by becoming slightly peripheral. Maintenance of the flight apparatus is very interesting. Although certainly adaptive at an earlier point in the history of the evolution of Carabidae or Coleoptera, it is in Broscini a plesiomorphic feature. Its retention in *Rawlinsius papillatus* was a functional necessity and reflects the precarious nature of the habitat.

Chorological Features

Itself a geographical relict, in the sense of its wide isolation from other broscines (see Fig. 12), and a phylogenetic relict, in the sense that it may be the lone survivor of a primitive broscine stock (see Simpson, 1944:144–145 and Brooks and McLennan, 1991:128 and 256–259, for discussions of the term “relict”), the genus *Rawlinsius* is known only from a region (the Sierra de Atoyac de Alvarez) that is rich in precinctive taxa (see, for example, Vargas-Fernandez et al., 1992; Llorente-Bousquets and Luis-Martinez, 1993). More generally, the mountains of southern Mexico, particularly the humid temperate forests (within which zone *Rawlinsius* occurs) are noted for an appreciable amount of precincting. Among such groups are various carabid lineages that are also geographical and/or phylogenetic relicts (Table 1). Within this geographical group, however, *Rawlinsius* is unique, being the only precinctive representative of its entire tribe to occur within this region.

These relict taxa are either monobasic or polybasic, ranging in rank from species to genus. The polybasic groups evidently have differentiated within the mountains of southern Mexico, whereas the monobasic groups either have not differentiated, or are sole survivors of the taxon to which each belongs.

The species *Nomius pygmaeus* (Dejean), with the most extensive part of its range occurring to the north, evidently has not differentiated. It is a relict at the population, rather than taxon, level. The monobasic *Galerita sulcipennis* group, subgenus *Tachalus* Ball and Nègre, and genus *Rawlinsius* are relicts at the taxonomic level, and may be survivors of lineages that were once more speciose. In any event, it seems reasonable to infer that *N. pygmaeus* is a relatively recent (Pleistocene age) arrival in southern Mexico, whereas the latter three groups arrived in the area at a substantially earlier time (Paleocene to Miocene).

As emphasized by Liebherr (1994:842), carabid taxa occupying the humid temperate forest zone in southern Mexico have either southern or northern roots. Of the taxa in Table 1, six are northern (including *Rawlinsius*) and five are southern in affinity. They represent three major distribution patterns recognized by Halffter (1987; see also Kohlmann and Halffter, 1990): the Nearctic pattern (for northern elements of more recent arrival), the Paleo-American pattern (for older northern elements), and the Meso-American Montane pattern (for southern elements reported here). Of the taxa listed in Table 1, then, *Nomius pygmaeus* represents the Nearctic pattern; *Tachalus*, *Rawlinsius*, and the *Hypherpes*-like taxa, the Paleo-

Table 1.—*Geographical relict taxa of Carabidae in southern Mexico.*

Taxon	Rank	Affinity		Reference
		North	South	
<i>Nomius pygmaeus</i> Dejean	Species	X		Ball, 1977:394–395 ¹
<i>Eucheila cordova</i> Ball and Shpeley	Species		X	Ball and Shpeley, 1983:802
<i>Galerita sulcipennis</i> Reichardt	Species group (monobasic)		X	Ball, 1985:317
<i>Tachalus</i> Ball and Nègre	Subgenus (monobasic) ²	X		Ball and Nègre, 1972:423
<i>Hypherpes</i> -like taxa ³	Three subgenera (polybasic)	X		Ball and Roughley, 1982
<i>Eripus</i> Dejean	Subgenus (polybasic)		X	Straneo and Ball, 1989:153
<i>Cyrtolaus</i> Bates	Genus (polybasic)		X	Lieberr, 1986:95
<i>Dyschromus</i> Chaudoir	Genus (polybasic)		X	Unpublished
<i>Rawlinsius</i> Davidson and Ball	Genus (monobasic)	X		This paper

¹ Bousquet and Larochelle (1993:158) provide a synopsis by states and provinces of the U. S. and Canadian range of this species: transcontinental in the northern boreal forest, southward to Georgia in the east, and southern Arizona and California in the west.

² For a different interpretation of the relationships of this taxon (as *Calthus ovipennis* Putzeys), see Lieberr (1994:848, fig. 10).

³ The subgenera included are: *Percolaus* Bates (Ball and Roughley, 1982:327), *Mayqferonia* Ball and Roughley (1992:336), and *Alloitriopus* Bates (Ball and Roughley, 1982:349). They belong to the northern genus *Pterostichus* Bonelli. Adults of the three subgenera are similar to one another in body form, and to the Nearctic subgenus *Hypherpes* Chaudoir. Relationships of these taxa to one another have not been established.

American pattern; and *Eucheila cordova* Ball and Shpeley, *Galerita sulcipennis* species group, *Eripus* Dejean, *Cyrtolaus* Bates, and *Dyschromus* Chaudoir, the Meso-American Montane pattern. The details of the Meso-American Montane pattern are of no further interest in the present context.

The relict status of the northern-based taxa suggests marked changes of some type that led to their isolation in the Mexican highlands, possibly drying of the intervening areas, with associated changes in vegetation. The fact that at least two different ages of dispersal are indicated suggests that either the climatic changes were cyclic in nature, or that the later-arriving *N. pygmaeus* had different adaptations from the earlier arrivals, and was thus able to spread southward. Ball and Nègre (1972:528) and more recent authors (e.g., Jameson 1990:412) hypothesized cyclic climatic changes within northern Mexico, resulting in conditions favorable for dispersal alternating with unfavorable conditions that resulted in more or less extensive range disruption with consequent differentiation of isolated populations that managed to survive in favorable areas or refugia.

We believe, then, that the ancestral Broscina were widespread in North America, and were possibly riparian in habitat preference. Unfavorable climatic conditions led to extinction of the Broscina over large parts of North America, with a single lineage persisting in southern Mexico. To the north, in western North America, one or more lineages survived and differentiated, but the descendants did not evolve the adaptations required to recover the whole of the ancestral range. Similarly, the Mexican lineage became highly specialized to live in association with fast-flowing water, and is thus unable to re-occupy the ancestral range in lowlands.

CONCLUDING REMARKS

The discovery of *Rawlinsius papillatus* was an exciting event in the development of knowledge of the Middle American carabid fauna. Additional populations of this species are not likely to be encountered casually and therefore the species may have a much wider range than known currently. Specimens probably will be found only at night, in very patchy microhabitats, mostly difficult of access. They are likely to be found only by the most energetic and persistent collectors, and then only with a good deal of luck. We hope that the discovery of this species will encourage adventurous collectors to search vigorously for further localities or additional species of *Rawlinsius* throughout southern Mexico, Central America, and perhaps even the northern mountains of South America. A taxon with such secretive and elusive members could turn up in any of the mountain ranges that add so much wonder and beauty to the tropics of the New World.

This remarkable relictual species forces attention on the area in which it is known to live—the Sierra de Atoyac de Alvarez. This mountain range, as well as the other parts of the Sierra Madre del Sur, gives evidence of a substantial amount of precinction, especially at higher altitudes. With extensive tracts of forest still intact, this mountain range would seem to be prime ground for establishment of an ecological reserve, as well as the focal point for extensive exploration of its fauna and flora. Undertaking such activities is a challenge for the government of Mexico, and for the Mexican biologists who are interested in biodiversity, the country's "rich biological patrimony" (Toledo and Ordoñez, 1993:775).

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